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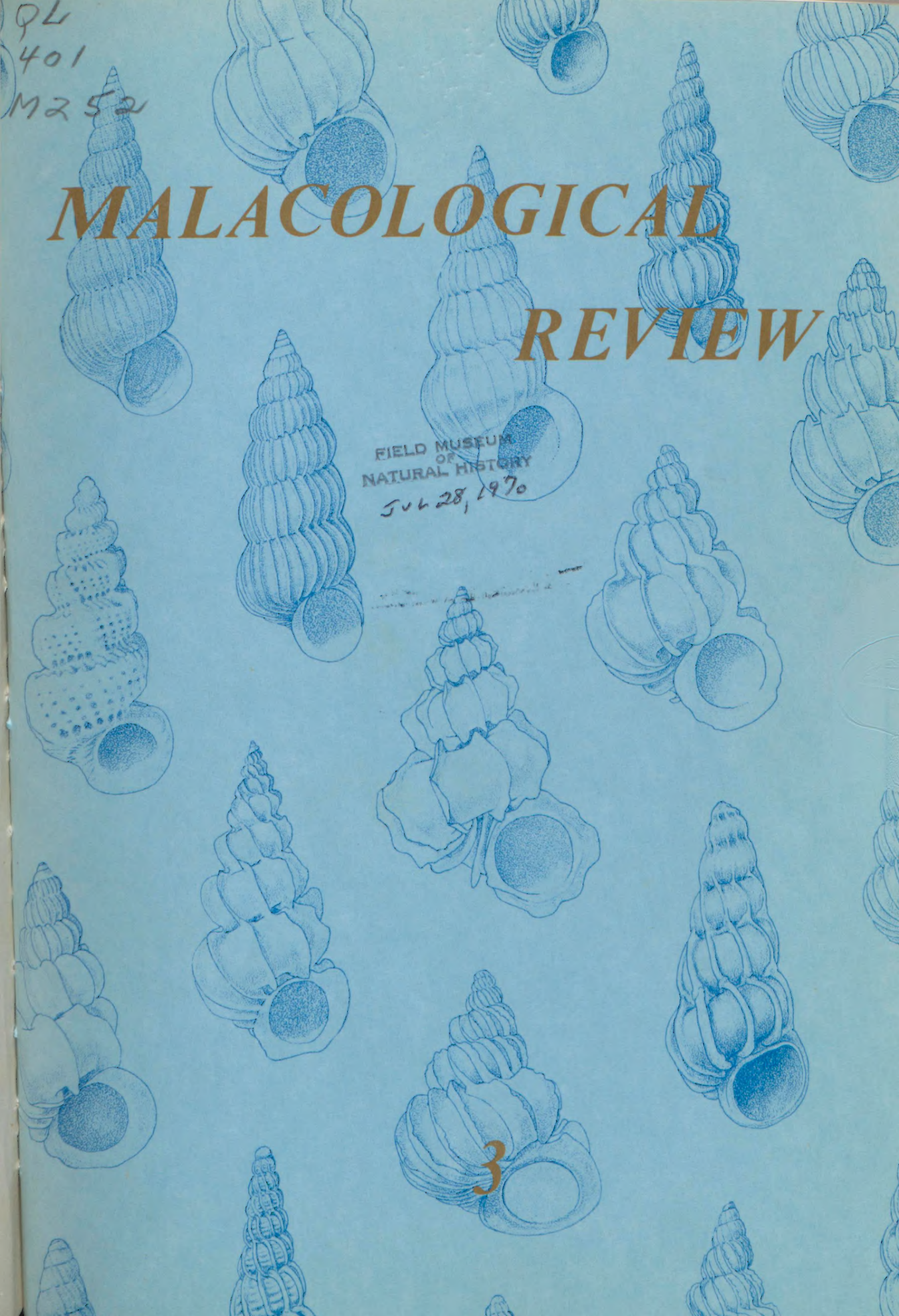

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AN IMMUNO-CYTOLOGICAL STUDY OF *BULINUS* s.s. (BASOMMATOPHORA: PLANORBIDAE)[1]

J. B. Burch[2] and G. K. Lindsay

ABSTRACT

The African genus *Bulinus* is of medical importance because some of its species are the intermediate hosts of human urinary schistosomiasis. In the subgenus *Bulinus* s.s., some species are susceptible to strains of *Schistosoma haematobium* and others are not. Therefore, accurate systematics at the specific or subspecific levels is of some consequence. The susceptible forms (*truncatus*-group species) seem to be linked to polyploid chromosome numbers, i.e., multiples of the basic 18 pairs found in the genus and in the non-susceptible *tropicus*-group of the subgenus.

Our general purpose was to investigate by an immunological method, antigenic similarities or eventual significant dissimilarities in *Bulinus* s.s. populations of the same and of different chromosome numbers. Foot muscle antigens from a total of 37 populations (18 with n=18, 13 with n=36, 5 with n=72 and 1 with n=54) from widely separated geographical locations were tested against antisera of diploid and polyploid species by the micro-Ouchterlony double diffusion test.

We were especially anxious to test whether or not populations that were cytologically *tropicus*-like (n=18), but morphologically *truncatus*-like according to radular characters ("arrowhead" shape of mesocones of 1st lateral teeth), were in reality *truncatus*-group (n=36) related, and not related to their geographically more closely located neighbors, *B. tropicus*.

There was good correlation between *Bulinus* s.s. chromosome numbers and immunological characteristics. In no instance did a species with one particular haploid chromosome number, when tested with antiserum for a species with a different chromosome number, fail to give a reaction for non-homologous antigens ("non-identity"). On the other hand, populations of the same chromosome number, with only 2 possible exceptions, showed no "non-identity" reaction.

When applied to current problems of taxonomy of *Bulinus* s.s., our studies show that radular characters, as currently used (i.e., whether or not the mesocones of the 1st lateral teeth have straight or bent lateral edges), have but little if any value for systematic placement of species into species groups.

INTRODUCTION

Recent studies by various authors (e.g., Mandahl-Barth, Wright, Brown, Schutte, etc., see Literature Cited, p 14) have contributed to our knowledge of the Planorbidae of Africa and the Near East. Nevertheless, malacologists are still encountering difficulties in their classifications, and it is evident that a great deal more should still be learned about the Planorbidae at all systematic levels. Some of the peculiar difficulties in classifying mollusks such as these have been discussed by Hubendick (1954) and, especially in regard to *Bulinus*, by Wright (1961). Of particular concern to us at the University of Michigan has been the planorbid

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[1]This paper was presented to the Symposium on Mollusks as Parasites or their Transmitters held in conjunction with the Third European Malacological Congress, Vienna, Austria, September, 1968.

[2]Supported by a Public Health Service Research Career Program Award (No. 5-K3-AI-19,451) and a research grant (AI 07279) from the National Institute of Allergy and Infectious Diseases, U.S. Public Health Service, and a Rockefeller Foundation travel grant (GA MNS 6325) to East Africa in 1965.

genus *Bulinus*, and, in particular, the *B. tropicus*, *B. truncatus* and the *B. natalensis*[3] species groups, because they form a rather closely related assemblage of species in one of which, i.e., the *truncatus* group, there occur polyploid chromosome numbers (Burch, 1964, 1967b; Natarajan, Burch & Gismann, 1965).

The planorbid genus *Bulinus* is found over most of the African continent where habitats are suitable for freshwater pulmonate snails. The genus is also found on the East African islands and selectively in many Mediterranean and Middle Eastern countries. The medical and veterinary importance of the genus lies in the fact that certain of its species are the intermediate hosts of the bloodflukes causing human urinary schistosomiasis.

The various bulinine species traditionally have been grouped into 3 taxa, formerly as genera, subsequently as subgenera: *Bulinus* s.s., *Physopsis* and *Pyrgophysa*[4]. In the subgenus *Bulinus* s.s., a biological (parasitological) difference has long been recognized between the northern and southern forms and has subsequently found its expression in the creation of 2 species groups: a more northern *truncatus* species group and a southern *tropicus* species group. Few of the taxa that have been assembled within these 2 species groups currently can be defined with any precision in terms of the limits of morphological variation and geographical distribution. Yet on both parasitological and cytological grounds, there do seem indeed to be 2 distinct groups that can be defined with some precision. The northern *truncatus* group is tetraploid (i.e., has the haploid chromosome number n=36) and, as far as known, is generally susceptible to infection with strains of *Schistosoma haematobium*, either under natural or experimental conditions. The more southern group is diploid (n=18) and except in one instance (Pitchford, 1965; Schutte, 1966), has not been found to be susceptible to human schistosome infection.

Assigning certain species to these groups has proven difficult for malacologists. For example, species that on the basis of certain morphological characters were first placed in one group by Mandahl-Barth (1957), only to be shifted by him later (1960, 1965) to another group are: *Bulinus guernei*, *B. natalensis* and *B. sericinus*. Characters that are currently being used to assign species to one or the other of the 2 species groups in question are: the shape of the mesocones of the 1st lateral tooth of the radula (arrowhead-shaped in *B. truncatus* and triangular in *B. tropicus*), the frequency of absence or atrophy of a male copulatory organ (a feature observed, in the past, in the *truncatus* group only, never in the *tropicus* group), to some extent the shape of the shell (Mandahl-Barth, 1965; Schutte, 1965, 1966; Brown, et al., 1967) and chromosome numbers, i.e., polyploidy (Burch, 1964, 1967b). Because of the apparent tenuousness of a classification based mainly on the variable radular characters mentioned above (the shape of the mesocone of the 1st radular tooth is often not clearcut nor constant in one and the same radula), and the seeming refutation of the definite cytological separation of

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[3] *B. natalensis* was recently separated from *B. tropicus* as a group because it possessed some characters in common with both the *B. truncatus* and *B. tropicus* groups (Brown, et al., 1967).

[4] Although there are certain nomenclatorial and other problems associated with this system (see Mandahl-Barth, 1957, who substituted "species groups" for the subgenera), it is nevertheless a traditional and convenient scheme which we hesitate to abandon for the time being. But, the type species of *Bulinus* Müller, *B. senegalensis* Müller, is apparently closely related to *Isidora forskalii* Ehrenberg, the type species of *Pyrgophysa*, and not to *B. truncatus* and *B. tropicus*, to which the name *Bulinus* s.s. is usually associated. Accordingly, *Pyrgophysa* becomes *Bulinus* proper and the first generic-group name available for the *truncatus-tropicus-natalensis* complex is *Isidora* Ehrenberg (*fide* Mandahl-Barth, and others, pers. comm.). However, there is a unanimous reluctance to adhere to strict application of the rules of nomenclature because of the confusion it would cause.

the 2 species groups (some specimens with arrowhead-shaped mesocones have only 18 pairs of chromosomes; see Schutte, 1966; Brown, et al., 1967), we decided to apply an immunological test that would give an indication as to whether south and central African *Bulinus* s.s. specimens resembling the tetraploid *B. truncatus* in certain characters, but having only 18 pairs of chromosomes, were more closely related to their diploid neighbors, or were more closely related to the generally more northern tetraploid *B. truncatus* species group. Concomitantly it was also tested, in 37 populations from widely separated geographical locations, whether or not *Bulinus* s.s. of the same chromosome number were antigenically similar or different, and whether or not different polyploid chromosome numbers would show significant antigenic differences or similarities. It is on the results of these immuno-cytological studies that the present paper is based. Preliminary brief accounts and abstracts of this work have appeared in Burch & Lindsay (1966, 1969) and Burch (1967c, d, 1968, 1969).

METHODS AND MATERIALS

Immunology

The immunological techniques used here are essentially the same as those adapted in this laboratory for molluscan studies by G. M. Davis and G. K. Lindsay, and described in detail by Davis (1968). Briefly, the procedures were as follows. Antibodies against snail antigens were produced in virgin female rabbits by introducing intravenously into the external marginal vein of each rabbit's ear 2 consecutive series of 5 one ml injections of snail foot protein (the antigen) in increasing concentrations, given on alternate days. The injections consisted of the supernatant liquid obtained after centrifugation of the homogenized snail foot tissue. The series were spaced 1 month apart and proceeded according to the following schedule:

Day	Weight in mg of tissue homogenized in 1 ml physiological saline
1, 39	15
3, 41	36
5, 43	75
7, 45	150
9, 47	214

Three, 5 and 10 days after the last injection 50 ml of whole blood were drawn from the rabbit from its external marginal ear vein. This blood was allowed to clot at room temperature for 30 minutes and cooled to 3° C for another 30 minutes to shrink the clot. The clot and the serum were placed into 2 different centrifuge tubes and spun at 3000 revolutions per minute for 30 minutes, during which time the temperature was maintained at 3° C. The sera from the 2 tubes were combined and similarly spun, after which the combined serum was collected and pushed through a 0.45μ Gelman sterilization filter into a sterile container. Finally, as an antibacterial agent, aqueous merthiolate (sodium-ethylmercurithiosalicylate) was added so that its final concentration in the serum was 0.0001%. This purified and sterile serum contained the antibodies.

Plates for the micro-Ouchterlony double diffusion test (e.g., see Ouchterlony, 1949) were prepared by fastening a glass ring 21 mm in inside diameter and 10 mm in height, to a microscope slide. The ring was stuck to the slide with a hot wax-gum mastic mixture. The semi-solid medium used to fill the rings was a 1% agar gel with 0.4% NaCl and 0.0001% merthiolate.

The gel medium was prepared by combining 50 gm of 2% deionized agar cubes, and 40 ml of 1% NaCl solution. This was placed in an autoclave and heated to 121° C at 10 lbs. pressure for 30 minutes. The gel solution was cooled to 40° C in a water bath. After adding 10 ml of the 1/1000 merthiolate solution, the gel was ready to use.

Two ml of the gel solution were added to each plate and allowed to cool, whereupon it solidified. The desired pattern of wells was cut into the gel using a special cutting device from a design of Dr. George W. Nace, University of Michigan. The plate was then ready for the immunodiffusion test.

As shown in Fig. 1, 4 wells were cut in the gel. In this type of well pattern 2 populations were tested against each other to show qualitative differences in their antigen-antibody reactions. Differences between homologous and heterologous extracts are seen by comparing the precipitin reactions between wells A and B and between wells B and C respectively. Proteins occurring in one population but not

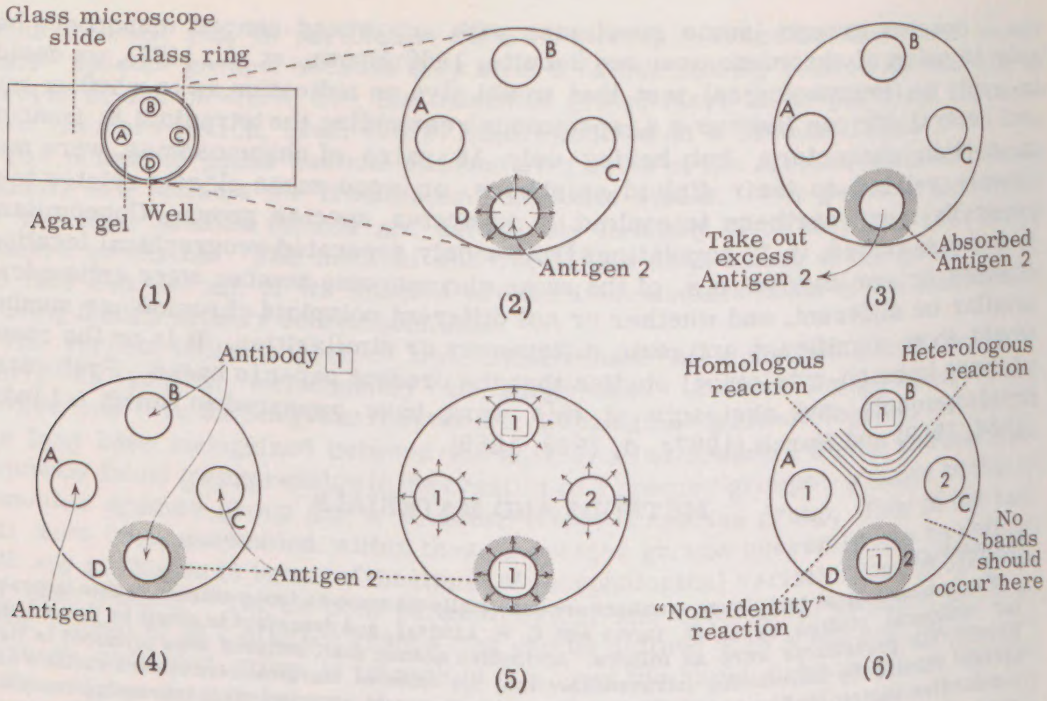

FIG. 1. Procedure for filling micro-Ouchterlony wells with antigen and antisera. "Heterologous reactions" between wells B and C in (6) are the precipitation reactions of homologous proteins between the antibody and a heterologous antigen, i.e., from a different population.

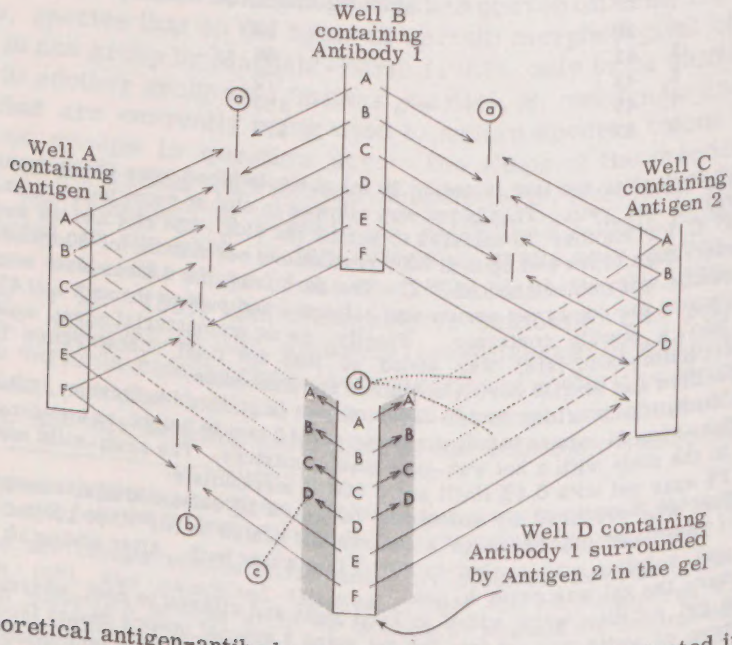
Well B containing Antibody 1
Well A containing Antigen 1
Well C containing Antigen 2
Well D containing Antibody 1 surrounded by Antigen 2 in the gel

FIG. 2. Theoretical antigen-antibody precipitin reaction, as illustrated in Fig. 1 (6), in a diagrammatic cut-away side view of the agar gel, showing where precipitation bands would occur and where they would not. ⓐ = antigen-antibody precipitation reactions; ⓑ = antigen-antibody precipitation reactions indicating a "non-identity" reaction between population 1 and population 2; ⓒ = common proteins between populations 1 and 2 are blocked in this region, i.e., the antibodies of population 1 are precipitated by the antigens of population 2; ⓓ = area where no precipitation bands are formed because antibodies do not meet their corresponding antigens.

in the other, can be observed by the reaction between wells A and D, because the antiserum in well D must pass through a surrounding barrier of heterologous antigen, allowing only those antibodies through to react that are not common to the 2 populations. Thus we could determine whether or not the 2 populations in question had developed immunologically detectable differences in foot muscle proteins in their evolutionary divergence. Therefore, the presence or absence of precipitin reactions between wells A and D were of prime interest to us in the current study. The space between wells C and D served as a control to indicate when the system was overloaded with antigen or antibody. Precipitation bands in this area indicates overload of antiserum in well D in relation to the pre-absorbed antigen around the well.

The procedure for filling the wells with antigen or antibody was as follows (Fig. 1). Well D was filled with the antigen of population 2, which was allowed to diffuse into the gel around the well for 24 hours. At the end of that time any residue of this antigen was removed from the well. Well A was then filled with the antigen of population 1, and wells B and D were filled with the antibodies of the same population. Well C was filled with the antigen of population 2. In preparing these plates, full-strength antisera were used. The fluid containing the antigen was the supernatant obtained from centrifuging 0.1 gm snail foot tissue homogenized in 1.0 ml physiological saline. The gels were allowed to incubate for 3-5 days to allow for the migration of protein fractions and then observed for the presence of precipitin bands. Fig. 2 illustrates a theoretical antigen-antibody scheme, also shown in the 6th illustration of Fig. 1, in which there are 6 visible bands precipitating in population 1, of which only 4 are shared by population 2.

Cytology

Ovotestes of specimens used for cytological examination, often the same specimens from which the antigens were prepared, were fixed in Newcomer's (1953) fluid. Chromosome counts were made from acetic-orcein squash preparations (La Cour, 1941), and were observed with a Nikon microscope using 100x (n.a. 1.25) oil immersion objectives and 10x oculars.

Snails

Antibodies were produced against 3 laboratory reared species, all with different chromosome numbers: *Bulinus tropicus tropicus*[5] (n=18), *B. coulboisi* (n=36), and *B.* sp. (n=72). The original source of the 3 species were as follows:

Bulinus tropicus tropicus (Krauss)[5]. Collected by J. B. Burch and J. Bosch from Crocodile Creek, Lake McIlwaine, Rhodesia, 2 April 1965. [Same as population no. 9 below.]

Bulinus coulboisi (Bourguignat). Collected by John McClelland at Mwanza, Tanzania, May, 1961. [Same as population no. 29 below.]

Bulinus sp. Collected by J. B. Burch from Lagaruba River, 16 miles north of Addis Ababa on the Debra Marcos Road, Ethiopia, September, 1965. [Same as population no. 37 below.]

Antigens were prepared from laboratory-reared specimens of the 37 populations of *Bulinus* s.s. listed below.

1. *Bulinus* sp. [n=18][6]. Collected by E. G. Berry at Senthiou Maleme, West Tamba Counda, Senegal, October, 1963. From laboratory stocks at the U.S. National Institutes of Health, Bethesda, Maryland, U.S.A.
2. *Bulinus* sp. [n=18][6]. Collected by E. G. Berry at Maka Sarakole, near Kortia (Tamba Counda), Senegal, October, 1963. From laboratory stocks at the U.S. National Institutes of Health, Bethesda, Maryland, U.S.A.
3. *Bulinus* sp. [n=18]. Collected by J. B. Burch from Lake Tana at Gorgora, Ethiopia, May, 1965.
4. *Bulinus* sp. [n=18]. Collected by J. B. Burch from a small stream 1 km south of Sulultu River, about 14 1/2 miles north of Addis Ababa on the Debra Marcos Road, Ethiopia, September, 1965.
5. *Bulinus* sp. [n=18]. Collected by J. B. Burch and D. S. Brown near Debra Berhan, Ethiopia, September, 1965.
6. *Bulinus* sp. [n=18]. Collected by J. B. Burch from Lake Bishoftu, near Debre Zeit, Ethiopia, September, 1965. We received a second collection from this locality from Aklilu Lemma, June, 1967.
7. *Bulinus* sp. [n=18]. Collected by J. B. Burch from a rock quarry, 10 km northwest of Asmara, Ethiopia, September, 1965.
8. *Bulinus tropicus alluaudi* (Dautzenberg) [n=18]. Collected by E. G. Berry from Mwe Tabari, Kenya, 1960.
9. *Bulinus tropicus tropicus* (Krauss) [n=18][5]. Collected by J. B. Burch and J. Bosch from Crocodile Creek, Lake McIlwaine, Rhodesia, April, 1965.
10. *Bulinus tropicus tropicus* (Krauss) [n=18][5]. Collected by J. B. Burch and J. Bosch from the head of False Creek, Lake McIlwaine, Rhodesia, April, 1965.

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[5]For difficulties in naming Rhodesian *Bulinus tropicus* and *B. natalensis* see Appendix, p 15.

[6]These diploid specimens were called *"Bulinus guernei"* by Natarajan, Burch & Gismann (1965); Burch & Lindsay (1966); and by Burch (1967b, c), because these N.I.H. laboratory stocks were so labelled (see Appendix, p 20). However, C. A. Wright later sent us specimens (n=36) that he considered to be true *B. guernei* (see population no. 28 in this list).

11. *Bulinus tropicus tropicus* (Krauss) [n=18][5]. Collected by J. B. Burch and J. Bosch at Fisherman's Bend, Lake McIlwaine, Rhodesia, April, 1965.

12. *Bulinus tropicus tropicus* (Krauss) [n=18][5]. Collected by J. B. Burch and A. Garnett from borrow pits at Marlborough, Salisbury, Rhodesia, April, 1965.

13. *Bulinus tropicus tropicus* (Krauss) [n=18][5]. Collected by V. de V. Clarke and C. J. Shiff near Salisbury, Rhodesia, April, 1961.

14. *Bulinus tropicus tropicus* (Krauss) [n=18][5]. Collected by J. B. Burch from a pond on Sinoia Road, about 5 miles north of Gwebi Agriculture College, about 25 miles from Salisbury, Rhodesia, March, 1965.

15. *Bulinus tropicus tropicus* (Krauss) [n=18][5]. Corundum mine, Concession, Rhodesia. Received from L. Husting, January, 1967.

16. *Bulinus tropicus tropicus* (Krauss) [n=18]. Collected by C. H. J. Schutte from De Villiers cement reservoir, Malelane, Nelspruit, Transvaal, Republic of South Africa, July, 1961.

17. *Bulinus natalensis* (Küster) [n=18][5]. Collected by J. B. Burch from a farm dam on Shamva Road, about 17 miles north of Salisbury, Rhodesia, April, 1965.

18. *Bulinus natalensis* (Küster) [n=18][5]. Collected by J. B. Burch and A. D. Harrison from a tributary of Gwebi River on Little England Farm, near Salisbury, Rhodesia, March, 1965.

19. *Bulinus truncatus* ssp. [n=36]. Corsica. Received from S. Grétillat, October, 1963.

20. *Bulinus truncatus truncatus* (Audouin) [n=36]. Sent by K. Y. Chu from Dezful, Iran, August, 1966.

21. *Bulinus truncatus truncatus* (Audouin) [n=36]. Sent by J. Massoud from Dezful, Iran, October, 1966.

22. *Bulinus truncatus truncatus* (Audouin) [n=36]. Collected by Fikry el Tawil from the Mena area, Giza Province, Egypt, March, 1961.

23. *Bulinus truncatus truncatus* (Audouin) [n=36]. Collected by W. B. DeWitt from the Iflaka Bilharzia Project area, Beheira Province, Egypt, February, 1965.

24. *Bulinus truncatus truncatus* (Audouin) [n=36]. Collected by E. A. Malek, from an irrigation canal in a pump scheme on the Blue Nile near Khartoum, Sudan, January, 1959.

25. *Bulinus truncatus* ssp. [n=36]. Collected by C. A. Wright from Belas, Western Aden Protectorate. Received in April, 1964.

26. *Bulinus truncatus rohlfsi* (Clessin) [n=36]. Collected by S. Grétillat on the Tagant Plateau, Mauritania, 1963.

27. *Bulinus truncatus rohlfsi* (Clessin) [n=36]. Collected by F. Wickremasinghe in the vicinity of Kumasi (Ashanti), Ghana, May, 1961.

28. *Bulinus guernei* (Dautzenberg) [n=36]. Collected by C. A. Wright, Gambia.

29. *Bulinus coulboisi* (Bourguignat) [n=36]. Collected by John McClelland at Mwanza, Tanzania, May, 1961.

30. *Bulinus coulboisi* (Bourguignat) [n=36]. Collected by J. B. Burch and A. D. Berrie at Koromji, Tanzania, April, 1965.

31. *Bulinus coulboisi* (Bourguignat) [n=36]. Collected by J. B. Burch and A. D. Berrie at Nyankunzi, Tanzania, April, 1965.

32. *Bulinus* sp. [n=54]. Collected by J. B. Burch from Sulultu River, 15 miles north of Addis Ababa on the Debra Marcos Road, Ethiopia, May, 1965. We received a second collection from this locality from Aklilu Lemma, June, 1967.

33. *Bulinus* sp. [n=72]. Collected by J. B. Burch and D. S. Brown, 3 km north of Debra Berhan on the road toward Debra Sina, Ethiopia, September, 1965.

34. *Bulinus* sp. [n=72]. Collected by J. B. Burch and D. S. Brown, 1 km north of Debra Berhan (from the Ancober Road junction), Ethiopia, September, 1965.

35. *Bulinus* sp. [n=72]. Collected by J. B. Burch and D. S. Brown, 14 km north of Sheno, Ethiopia, September, 1965.

36. *Bulinus* sp. [n=72]. Collected by J. B. Burch and D. S. Brown, 4 km south of Sheno, Ethiopia, September, 1965.

37. *Bulinus* sp. [n=72]. Collected by J. B. Burch from Lagaruba River, 16 miles north of Addis Ababa on the Debra Marcos Road, Ethiopia, September, 1965.

RESULTS

We paid special attention to those antigen-antibody reactions that indicated presence or absence of non-homologous proteins between each of the population pairs we were testing (Fig. 4), because this test gives us the best indication of closeness of relationship. Tables 1 and 2 show the occurrence of "non-identity"

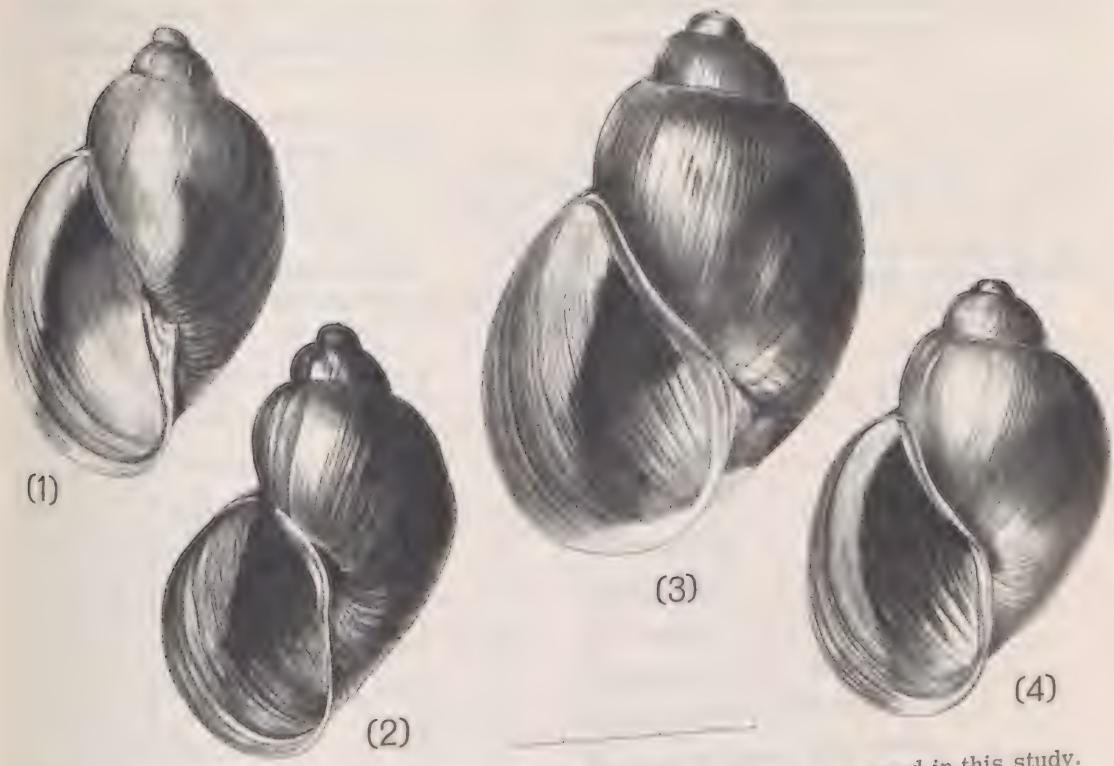

FIG. 3. Shells of lab-raised offspring of 4 species of *Bulinus* s.s. used in this study. Each shell was carefully chosen to represent the "typical" shell-shape of its population.
(1) *Bulinus tropicus tropicus* [n=18], population 14 (see p 6);
(2) *B. truncatus truncatus* [n=36], population 23 (see p 6);
(3) *B.* sp. [n=54], population 32 (see p 6);
(4) *B.* sp. [n=72], population 36 (see p 6). [Scale in mm]

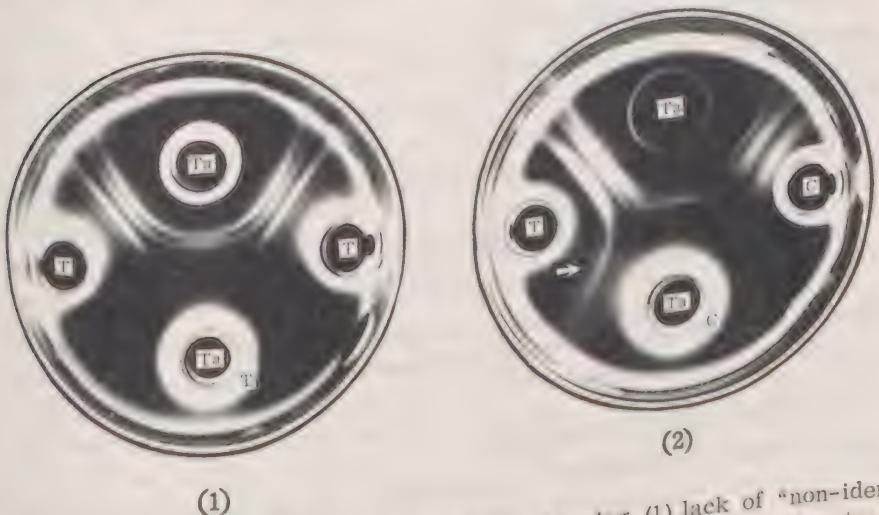

FIG. 4. Examples of agar gel diffusion plates, showing (1) lack of "non-identity" reaction, and (2) "non-identity" precipitation reaction (arrow), T = *Bulinus tropicus tropicus* antigen [n=18; population 9, see p 5]; Ta = *B. t. tropicus* antiserum; C = *B. coulboisi* antigen [n=36; population 29, see p 6]; Ca = *B. coulboisi* antiserum.

TABLE 1. "Non-identity" reactions, observed in the micro-Ouchterlony immunodiffusion test, between antigens of diploid *Bulinus* s.s. and antisera of diploid, tetraploid and octoploid *Bulinus* s.s.

Population no. *	Species of *Bulinus* furnishing antigen	Country	Haploid chromosome number (n)	Occurrence of "non-identity"++ reaction		
				n=18 antiserum	n=36 antiserum	n=72 antiserum
1	*B.* sp.**	Senegal	18	o‡	–	2
2	*B.* sp.**	Senegal	18	o	–	–
3	*B.* sp.	Ethiopia	18	–	–	3 + 1
4	*B.* sp.	Ethiopia	18	o	–	–
5	*B.* sp.	Ethiopia	18	o	2	–
6	*B.* sp.	Ethiopia	18	o	1 + 2	3 + 1
7	*B.* sp.+	Ethiopia	18	2 + 2+	3 + 1	2 + 1
8	*B. tropicus alluaudi*	Kenya	18	o	3	3
9	*B. tropicus tropicus*††	Rhodesia	18	o	3 + 2	2 + 1
10	*B. tropicus tropicus*††	Rhodesia	18	o	2 + 1	2
11	*B. tropicus tropicus*††	Rhodesia	18	o	3	–
12	*B. tropicus tropicus*††	Rhodesia	18	o	2 + 2	–
13	*B. tropicus tropicus*††	Rhodesia	18	o	3 + 1	2 + 1
14	*B. tropicus tropicus*††	Rhodesia	18	o	2 + 1	2
15	*B. tropicus tropicus*††	Rhodesia	18	o	3 + 2	–
16	*B. tropicus tropicus*	S. Africa	18	o	3 + 2	2
17	*B. natalensis*††	Rhodesia	18	o	3	–
18	*B. natalensis*††	Rhodesia	18	o	2	2

* Consecutive numbers as in list p 5-6.

** These diploid specimens were called "*Bulinus guernei*" in several previous publications (see footnote 6, p 5).

++ In terms of number and intensity of "non-identity" precipitation bands: 1 = weak; 2 = medium; 3 = strong (3 + 2 = two bands occurred, one strong and one medium in intensity).

‡ o = no "non-identity" reaction occurred between wells A and D.

– Test not made.

+ See p 9 regarding tests with this population.

†† For difficulties in naming Rhodesian *Bulinus tropicus* and *B. natalensis*, see Appendix, p 15.

TABLE 2. "Non-identity" reactions, observed in the micro-Ouchterlony immunodiffusion test, between antigens of polyploid *Bulinus* s.s. and antisera of diploid, tetraploid and octoploid *Bulinus* s.s.

Population no. *	Species of *Bulinus* furnishing antigen	Country	Haploid chromosome number (n)	Occurrence of "non-identity" reaction		
				n=18 antiserum	n=36 antiserum	n=72 antiserum
19	*B. truncatus* ssp.	Corsica	36	3 + 1 ++	o ∓	2
20	*B. truncatus truncatus*	Iran	36	2 + 1	o	2
21	*B. truncatus truncatus*	Iran	36	2 + 1	o	2
22	*B. truncatus truncatus*	Egypt	36	3 + 2	o	-
23	*B. truncatus truncatus*	Egypt	36	3 + 2	o	2
24	*B. truncatus truncatus*	Sudan	36	2 + 2	o	2
25	*B. truncatus* ssp.	W. Aden	36	2	o	-
26	*B. truncatus rohlfsi*	Mauritania	36	1 + 2	o	-
27	*B. truncatus rohlfsi*	Ghana	36	1 + 1	o	2
28	*B. guernei*	Gambia	36	2 + 1	o	-
29	*B. coulboisi*	Tanzania	36	3 + 2	o	3 + 1
30	*B. coulboisi*	Tanzania	36	1 + 2	o	-
31	*B. coulboisi*	Tanzania	36	3 + 1	o	-
32	*B.* sp.	Ethiopia	54	2 + 2	-	2 + 2
33	*B.* sp.	Ethiopia	72	1 + 1	-	-
34	*B.* sp.	Ethiopia	72	2 + 1	-	-
35	*B.* sp.	Ethiopia	72	1 + 1	2	o
36	*B.* sp.	Ethiopia	72	1 + 1	2 + 2	o
37	*B.* sp.	Ethiopia	72	1 + 1	2 + 1	o

*
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} See footnotes, Table 1, p 8.

bands between wells A and D of the micro-Ouchterlony plates. It is of particular significance that in no instance where tests were made did reactions of the "identity" type("identity" indicated by o in the tables) occur between populations of 2 different chromosome numbers, and that, but for 1 exception, "non-identity" reactions (shown in Tables 1 and 2 in terms of numbers indicating the relative strength of their antigen-antibody reactions) occurred only between populations having different chromosome numbers, whereas populations of the same chromosome number showed only "identity".

The exception mentioned above was *Bulinus* sp. (n=18) from near Asmara, Ethiopia (no. 7, p 5), which exhibited a relatively strong "non-identity" reaction

with antiserum of *B. tropicus* (as well as with the other 2 antisera). The chromosome numbers of various specimens of these Ethiopian snails were determined (as routinely done in all our tests) at the time the immunological studies were conducted. All were n=18. However, a year later some specimens in the stock tank had chromosome numbers of *truncatus*-group species (n=36). Since a mixture of n=18 and n=36 antigens would produce "non-identity" reactions with both n=18 and n=36 antisera, immunological tests should be repeated with fresh-collected and cytologically-known specimens from the Asmara locality. (For a second possible exception, see Appendix, p 16.)

DISCUSSION

For several years the senior author has been engaged in cytotaxonomic studies of snails of the genus *Bulinus*, the intermediate hosts of schistosomes causing human urinary and also ungulate schistosomiasis in Africa and the Near East. Such studies have a practical value because they have elucidated a cytological basis correlative to or responsible for the biological separation of the susceptible *truncatus* and insusceptible *tropicus* species groups. Parasitologically these 2 groups have been distinguished for some time (e.g., see Gismann, 1954; WHO, 1956; Abdel Azim & Gismann, 1956; Dawood & Gismann, 1956; Cridland, 1957). *Truncatus* group species are actual or potential hosts for the northern strains of schistosomes of the *haematobium* group (having terminal-spined eggs), whereas the *tropicus* group species have proven, but for one instance (Pitchford, 1965; Schutte, 1966), refractory to infection by all strains under experimental conditions.

Despite the clearcut cytological and apparent parasitological separation of these 2 snail species groups, they have proven very difficult for malacologists and other field workers to distinguish morphologically. Mandahl-Barth (1957, 1960, 1965) suggested that the shape of the mesocone of the lateral radular teeth, with some reservations, could separate the 2 groups. Schutte (1965, 1966) and Brown, et al., (1967) have assigned significant weight to this character to show that *truncatus*-like populations occur commonly in S. Africa, although when known, these specimens had cytological characters (n=18) of the southern *tropicus* group. Brown, et al., (1967) established a 3rd species group, the *B. natalensis* group, for these troublesome forms. Therefore, we were anxious to test whether or not populations that were cytologically *tropicus*-like, but morphologically (mesocone) *truncatus*-like, were in reality *truncatus*-group related, and not perhaps more closely related to their geographically more closely located neighbors, *B. tropicus*.

In the 37 species or populations of *Bulinus* s.s. that we studied, we found a clear-cut correlation between chromosome numbers and relationships shown by the immunological antigen-antibody reactions. In no instance did we find that a species with a haploid chromosome number of 18 was closely related (antigenically) to a *truncatus* group (n=36) species, or to a species with a haploid chromosome number of 72, or that a species with a haploid chromosome number of 36 or 72 was closely related to a *tropicus* group (n=18) species. Distinct and strong non-homologous protein reactions occurred every time we tested a species of one of these chromosome number groups against that of the other chromosome number group. *Bulinus natalensis* (n=18), first placed in synomony with *B. tropicus tropicus* by Mandahl-Barth (1957), but later (1965) shifted to the *truncatus* species group on the basis of the shape of the mesocone of the 1st lateral radular tooth, shows strong immunological dissimilarities to the *truncatus* group, whereas no non-homologous foot muscle proteins were found when its antigens were tested

with antiserum of *B. tropicus* (n=18). Therefore, we conclude that the radular characters as presently used by malacologists have but little if any value for the systematic placement of *Bulinus* s.s. species into one or the other of these 2 species groups. The answer to the question raised by Brown, et al., (1967) as to which are the more important diagnostic characters, i.e., egg-mass proteins and cytology or radular mesocone shape and relative degree of atrophy or absence of a terminal male copulatory organ, seems to point to biochemistry and chromosome number. The question might be further elucidated when we have the opportunity to test, cytologically and immunologically, other nominal species, such as *Bulinus depressus*, also with 18 pairs of chromosomes and radular mesocone characters similar to *B. truncatus*.

On immunological grounds (non-identity reactions), the *Bulinus* s.s. specimens with 72 pairs of chromosomes would seem to belong to a 3rd heretofore unrecognized species group, but yet, certain aspects of their biochemistry (egg proteins and foot-muscle esterases)[7] are very similar to those of *B. truncatus*. *Bulinus* sp. (n=18) specimens from near Asmara, Ethiopia, would appear to belong to still a fourth group (if further tests confirm that this population does indeed show "non-identity" with n=18 antisera [see p 9]), or perhaps they merely belong to another clearly distinct species of the *B. tropicus* group.

As for the specimens whose antigens and antisera did not show "non-identity" reactions, the possibility exists, of course, that they do actually belong to populations of one and the same widespread "species." If this were the case, then *Bulinus truncatus* would extend westward to Gambia (see Fig. 5) and would include the nominal species there currently called "*B. guernei*," and it would also extend south of the Sahara to Tanzania, and would include the nominal species there currently called *B. coulboisi*. *B. tropicus* would include populations as far north as Debra Berhan, Ethiopia, and as far west as Senegal, as well as possibly some populations currently assigned to the nominal species *B. natalensis*. On the other hand, regardless of lack of immunological dissimilarity, there are indications that typical *B. natalensis*[8] may be a distinct species, but that its diagnostic characters have not yet been described adequately, and that certain *B. tropicus* populations have been confused with it.

Recent results from C. A. Wright's laboratory indicate that additional biochemical tests do not correlate with the separation of the *tropicus* and *truncatus* groups by the radular teeth criteria. Wright, Klein & Eccles (1967) found that the radular teeth of *Bulinus succinoides* from Lake Malawi (= Lake Nyasa), although unusual, were "definitely more like the arrowhead type of the *truncatus* group, rather than the simple triangle of the *tropicus* complex." Additionally, the shell bore some resemblance to members of the *B. truncatus* group, specifically to *B. coulboisi* and *B. transversalis*, and the occurrence of aphallic specimens and the polymorphism of mantle pigmentation suggested affinities with the *truncatus* group. Nevertheless, they found 18 bivalents at male diakinesis and an electrophoretic pattern of egg-proteins that "resembles closely that characteristic for the *tropicus* group." Also, in immunological tests, *B. succinoides* "antigens yield results similar to those of *B. tropicus*," and not to those of *B. truncatus*.

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[7] See Wright & Ross (1965) and Burch & Lindsay (1967).

[8] Burch (1964), Natarajan, Burch & Gismann (1965) and Brown, et al. (1967) reported several extra chromosomal elements present in individuals of species identified as *Bulinus natalensis* or belonging to the *B. natalensis* group. These extra elements may have been present because of past incompatibility between dissimilar chromosomal complements. There exists the possibility that these specimens were hybrids (as suggested by Burch, 1964) between 2 sibling species, perhaps *B. tropicus* and *B. natalensis*. Also, Pitchford's (1965) and Schutte's (1966) diploid snails susceptible to various schistosomes would seem to be physiologically different from the refractory *B. tropicus*.

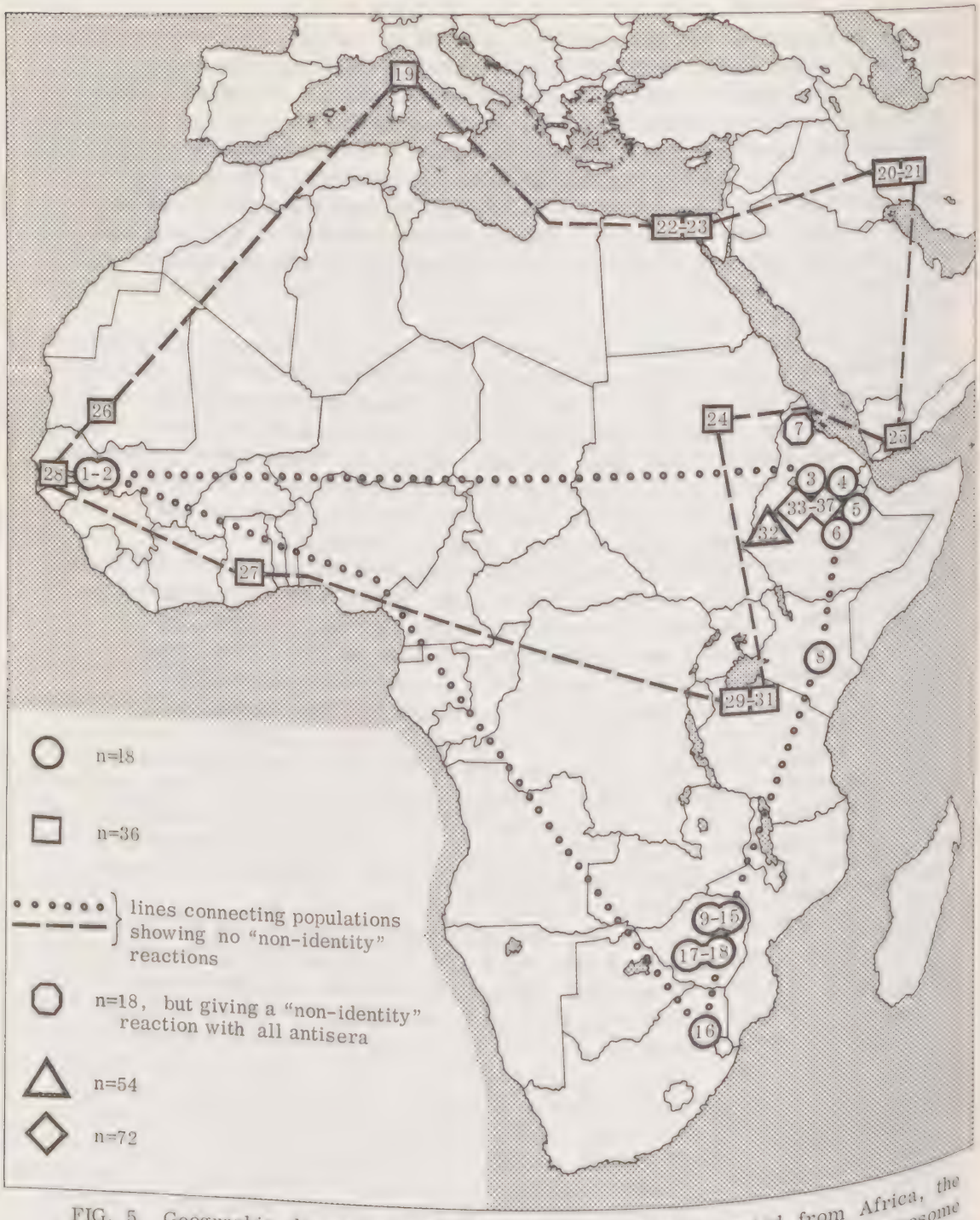

FIG. 5. Geographic distribution of *Bulinus* s.s. populations tested from Africa, the Mediterranean area and the Middle East, showing the correlation between chromosome numbers and immunological similarities. Numbers inside symbols correspond to the consecutive numbers arbitrarily assigned to the populations listed on p 5-6.

The susceptibility of the diploid Nelspruit population of *Bulinus* s.s. (*B. natalensis?*) to southern and northern forms of schistosomes of the *Schistosoma haematobium* group reported by Pitchford (1965) and Schutte (1966) is most interesting. The polyploid *B. truncatus* species group must have arisen from such susceptible diploid forms; *B. truncatus* is the only member of the *Bulinus* group that migrated north of the Sahara and in the northern part of the genus' distribution, it transmits

TABLE 3. Susceptibility of some *Bulinus* s.s populations to an Egyptian strain of *Schistosoma haematobium* (from Lo, 1968).

Population no. *	Species	Haploid chromosome number (n)	Experimentally infected
5	*B.* sp.	18	o
6	*B.* sp.	18	o
7	*B.* sp.	18	o
8	*B. tropicus alluaudi*	18	o
9	*B. tropicus tropicus*††	18	o
10	*B. tropicus tropicus*††	18	o
11	*B. tropicus tropicus*††	18	o
12	*B. tropicus tropicus*††	18	o
13	*B. tropicus tropicus*††	18	o
14	*B. tropicus tropicus*††	18	o
16	*B. tropicus tropicus*	18	o
18	*B. natalensis*†† x	18	o
19	*B. truncatus* ssp.	36	+
20	*B. truncatus truncatus*	36	+
21	*B. truncatus truncatus*	36	+
24	*B. truncatus truncatus*	36	+
25	*B. truncatus* ssp.	36	+
26	*B. truncatus rohlfsi*	36	+
27	*B. truncatus rohlfsi*	36	+
28	*B. guernei*	36	+
29	*B. coulboisi*	36	+
37	*B.* sp.	72	+

*, †† See footnotes, Table 1, p 8.

x For additional infectivity studies of *B. natalensis*, see Lo, Burch & Schutte, 1970.

S. haematobium and *S. bovis*.

Lo (1968) studied the susceptibility of many of our laboratory populations of *Bulinus* to infection with an Egyptian strain of *Schistosoma haematobium*[9]. His results are listed in Table 3, since they have pertinence to our own studies, in

[9] Past inferences (Burch, 1964, 1967b, c; Natarajan, Burch & Gismann, 1965; Burch & Lindsay, 1966, 1967; Burch & Natarajan, 1966; Brown, et al., 1967) from our laboratory about the susceptibility of various bulinine species were inferred from the literature (Gismann, 1954; Abdel Azim & Gismann, 1956; Dawood & Gismann, 1956; Cridland, 1955, 1957).

that he used the same laboratory populations that we studied. It is of special note that in no instance was Dr. Lo able to experimentally infect a diploid (n=18) species, and in every attempt he was able to infect the polyploid species, including the octoploid (n=72) species from Ethiopia. Therefore, the only reported population of diploid (n=18) *Bulinus* s.s. (*B. natalensis?*) that has been successfully infected with *S. haematobium* is one found in outdoor aquaria at the Nelspruit Bilharzia Research Unit laboratory (Pitchford, 1965; Schutte, 1966).

One of the populations (no. 18, p 6) that we tentatively called *Bulinus natalensis* was subjected to *Schistosoma haematobium* miracidia of our Egyptian strain by Dr. Lo, but no specimens were infected, perhaps indicating that our snails were not *B. natalensis* after all (if *B. natalensis* proves to be commonly susceptible to schistosome infection), or at least not that particular susceptible strain.

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APPENDIX

1. Identification of Rhodesian *Bulinus tropicus* and *B. natalensis* in this paper

The proper identification of our *Bulinus tropicus* and *B. natalensis* from Rhodesia has caused us considerable concern. Our material from a tributary of the Gwebi River on Little England Farm (erroneously called "New England Farm" in Burch, 1964; Natarajan, Burch & Gismann, 1965) near Salisbury, Rhodesia, was originally called *B. tropicus tropicus*, but later (Burch & Lindsay, 1967 [one of the "four Rhodesian populations"]) we changed the name to *B. natalensis*, because specimens from that same spot had been previously so identified by Mandahl-Barth (1965 p 41) (*fide* A. D. Harrison,

pers. comm.). Our specimens from Lake McIlwaine, Rhodesia were originally called *B. natalensis* (Burch, 1964; Natarajan, Burch & Gismann, 1965), as were also the laboratory raised descendants of specimens from that lake (Burch & Lindsay, 1966, 1967; Burch, 1967c, d, 1968), because Mandahl-Barth (*loc. cit.*) had previously considered specimens sent to him from that lake to be *B. natalensis*. Later Dr. Mandahl-Barth kindly inspected lab-raised descendants of these populations [Lake McIlwaine (nos. 9, 10, 11) and tributary of Gwebi River (no. 18)]. With reservations, he considered these[10] (and others) to be: "*B. tropicus*, because all specimens are euphallic, have a straight columella, no traces of spiral lines, and radula more or less of the *tropicus* type. However, in three samples, viz. Marlborough [no. 12], Little England Farm [no. 18] and Shamva Road [no. 17], the lateral teeth seem to be intermediate between *tropicus* and *natalensis*, but this is hardly sufficient to call them *natalensis* unless you have found that the chromosome[s] . . . support this possibility."

Mr. C. H. J. Schutte also inspected lab-raised descendants of the above Rhodesian populations (plus populations no. 8 and no. 16), and kindly made the following comments: "I have examined only a limited number of specimens from each sample and my general impression is of *tropicus*. The three samples identified as *natalensis* are placed in that nominal group with some reservation as no aphallic specimens were found, none of the radulae have the arrowhead character as marked as do most of our South African samples placed in the *natalensis* group and their shells are not of the low-spired form usually found in South African *natalensis*. This latter could be the result of modification under lab conditions (see Schutte, 1966). It would of course be necessary to know the chromosome numbers if there were a question of both the *natalensis* and *truncatus* groups involved." Mr. Schutte also got the opinions of Dr. D. S. Brown regarding specimens from these same samples, and Dr. Brown's opinions agree with his. Their tentative identifications are shown in column 7 of Table 4.

It is noted here that 2 of the samples that Mr. Schutte tentatively identified as belonging to the *Bulinus natalensis* group, were samples that Dr. Mandahl-Barth mentioned to have lateral radular teeth intermediate between *B. tropicus* and *B. natalensis*. Therefore, in this current paper, we are tentatively calling our Rhodesian snails of these 2 lots (no. 17, Shamva Rd.; no. 18, trib. of Gwebi R.) *B. natalensis*, although we realize the possibility that they may not be significantly different from *B. tropicus*.[11]

The difficulties of providing a name for our Rhodesian *Bulinus* s.s. specimens emphasizes the great morphological similarity of *B. tropicus* and *B. natalensis*, and the difficulties inherent in using the occurrence of a certain proportion of aphallic individuals and characters such as the variable radular tooth cusp shapes or shell shapes in separating such closely related bulinine species as *B. tropicus* and *B. natalensis*, if indeed they are 2 distinct "species."

2. Immunological reactions of "*Bulinus guernei*" from Senegal

When we received specimens of Senegalese *Bulinus "guernei"* from Dr. Elmer G. Berry (he collected them in October, 1963; we observed their chromosomes in 1964), we determined the chromosome numbers of the 6 specimens we then examined as n=18 (Natarajan, Burch & Gismann, 1965). Later (Burch & Lindsay, 1966; Burch, 1967c), when we tested antigens from their descendants reared in our laboratory aquaria against *B. tropicus* (n=18) antisera, we observed no "non-identity" reactions. At that time we did not have satisfactory antisera for the *B. truncatus* group (n=36). Testing their antigens against *B.* sp. (n=72) antisera, we did obtain a "non-identity" reaction. Both immunological results were as expected for a species with 18 pairs of chromosomes. Thus, we concluded that these *B. "guernei"* belonged to the *B. tropicus* group.

However, in 1967 we prepared antisera against *Bulinus coulboisi* (n=36) antigens, against which we tested antigens of specimens from our "*B. guernei*" tanks. The specimen's antigens showed "non-identity" with *B. coulboisi* antisera, as expected, but this time also when tested against our *B. tropicus* antisera. We determined the chromosome numbers of 6 specimens from our tanks, all of which showed n=36. We surmised that the *truncatus* group species now contained in the *B.*

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[10] Dr. Mandahl-Barth looked at 10 lots, the lab-raised descendants from my localities 8-14, 16-18 (p 5,6). He considered all of these to be *Bulinus tropicus* (see Table 4, column 6), with the reservations mentioned here. He emphasized ". . . that it is almost impossible to identify specimens of *Bulinus* that have been kept in captivity for several generations. They change so much that nearly all distinctive characters become blurred." Other planorbid snails are known to exhibit similar morphological changes when raised for several generations in the laboratory (e.g., see Richards, 1964).

[11] After this study was made, we were able to obtain live Zululand (Lake Sibayi) specimens of *Bulinus natalensis* through the courtesy of Dr. C. A. Wright which had been determined by Drs. C. Mandahl-Barth and D. S. Brown as being more surely representative of *B. natalensis* (see Burch & Lindsay, 1970).

TABLE 4. Current nomenclature of Rhodesian populations of *Bulinus* s.s. (n=18) (last column) contrasted to past nomenclature for specimens from these localities

Population no. (see p 5-6)	Locality	Mandahl-Barth, 1965	Burch, 1964; Natarajan, Burch & Gismann, 1965	Burch & Lindsay, 1966, 67; Burch, 1967c, d	Mandahl-Barth (pers. comm.)	Schutte (pers. comm.)	This paper*
		Original collection		Laboratory-raised offspring			
9	Croc. Cr., L. McIlwaine	Lake McIlwaine		*natalensis*	*tropicus*	"*tropicus* group"	*t. tropicus*
10	False Cr., L. McIlwaine	*natalensis*	*natalensis*	*natalensis*	*tropicus*	"*tropicus* group"	*t. tropicus*
11	Fisherman's Bend, L. McIlwaine			*natalensis*	*tropicus*	"*tropicus* group"	*t. tropicus*
12	Marlborough, Salisbury			*t. tropicus*	*tropicus*	"*tropicus* group"	*t. tropicus*
13	nr. Salisbury				*tropicus*	"*tropicus* group"	*t. tropicus*
14	Sinoia Rd., ca. 25 mi. n. Salisbury			*t. tropicus*	*tropicus*	"*natalensis* group"	*t. tropicus*
17	Shamva Rd., ca. 17 mi. n. Salisbury				*tropicus*	"*natalensis* group"	*natalensis*
18	Trib. Gwebi R.	*natalensis*	*t. tropicus*	*natalensis*	*tropicus*	"*natalensis* group"	*natalensis*

*The use of names here (last column) is based on Dr. Mandahl-Barth's and Mr. Schutte's comments on our lab-raised specimens. Populations 14, 17 and 18 are a problem because Dr. Mandahl-Barth indicated they were *B. tropicus*, whereas Mr. Schutte referred them to the "*natalensis* group." Since populations 17 and 18 contained specimens with intermediate lateral teeth according to Dr. Mandahl-Barth, we are calling them *B. natalensis* here.

guernei tank had perhaps been inadvertently introduced since our earlier cytological and immunological studies.

In order to check this, we again tested antigens of specimens from our "*Bulinus guernei*" tanks against our 3 antisera, and fixed the ovotestis of each of the 12 specimens needed to produce the necessary antigen material. We obtained "non-identity" reactions with each of the antisera. Of the 8 specimens from which we could determine chromosome numbers, all had 36 pairs of chromosomes. We ran these tests again, with similar results. This time we could determine chromosome numbers of 12 of the 18 specimens needed to obtain antigen, all of which had 36 pairs of chromosomes.

We might conclude from the above that our n=36 specimens from Senegal were neither *Bulinus truncatus* nor *B. coulboisi* introduced from our stock tanks of those species, but that the snail concerned might belong to yet another unrecognized species complex, or be a more clearly demarked species of the *B. truncatus-coulboisi* complex. If such were the case, a possible explanation for the occurrence, at different times, of n=18 and n=36 specimens in our stock tanks of "*B. guernei*" is that the original collection of specimens contained 2 species, one with 18 pairs of chromosomes, and one with 36 pairs of chromosomes, the former in greater abundance. The n=18 species gradually died off, but the n=36 species survived and reproduced. However, since we could not determine the chromosome numbers of *every* specimen pooled to obtain our test antigens, the possibility still exists that a few n=18 specimens were mixed with the n=36 specimens. It is desirable that further immunotaxonomic studies be conducted on other populations of Senegalese and other West African bulinine snails.

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CYTOLOGICAL STUDIES OF INDIAN MOLLUSKS: CHROMOSOMES OF SOME OPISTHOBRANCHS FROM PORTO NOVO, SOUTH INDIA[1]

R. Natarajan

ABSTRACT

This study deals with the chromosomes of 7 species of opisthobranchiate mollusks from Porto Novo, South India. In the Nudibranchia, *Thordisa crosslandi* (Doridiidae) was found to have 13 pairs of chromosomes. In the Anaspidea, *Aplysia benedicti* and *Bursatella leachii* (Aplysiidae) had n=17, while in the Notaspidea, one species of *Pleurobranchaea* (Pleurobranchidae) was found to have a haploid number of 13. In the Cephalaspidea, *Haminoea crocata* (Atyidae) had 17 bivalents during meiosis, but *Cryptophthalmus olivaceous* (Smaragdinellidae) had 18. In the primitive cephalaspidean *Hydatina velum* (Hydatinidae) the haploid number of 15 was found.

The present findings are in agreement with previous ones on chromosomes of opisthobranchs from the Indo-Pacific area, confirming the extreme conservatism in regard to change in chromosome number in the Opisthobranchia. The family Smaragdinellidae seems to be characterised by the haploid chromosome number 18, which perhaps supports the view that the order Basommatophora (x=18) was derived from the cephalaspid superfamily Philinacea.

The haploid chromosome number 15 (*Hydatina*) is reported for the 1st time. It may be significant that this number not only helps bridge the wide gap between the haploid chromosome number 13 of the Nudibranchia and 17 of most other opisthobranchs, but it also occurs in a very primitive cephalaspidean family (the Hydatinidae).

INTRODUCTION

Inaba (1959, 1961), Burch (1965, 1967), Burch & Natarajan (1967), Inaba & Saiki (1967), and Patterson (1969) have reviewed the available information on chromosomes of opisthobranch mollusks. Relatively few species have been studied because of the difficulties in their collection and identification. Apart from 2 species of Soleolifera (Natarajan, 1959, 1960), chromosomes of opisthobranchs from the Indian region have not received any previous attention. Information is presented here on 7 species of opisthobranch mollusks collected from the inshore waters of Porto Novo, South India.

MATERIALS AND METHODS

All the species used in this study were collected in the Bay of Bengal off the Porto Novo coast during August and September, 1967 and 1968. The specimens were brought alive to the laboratory, where the gonads were fixed and preserved in Newcomer's (1953) and Carnoy's (1887) fluids for study by the aceto-orcein squash technique (La Cour, 1941). All observations were made on the meiotic cells of spermatogenesis, using an Olympus (Japan) ECE-Tr microscope equipped with a 100x (n.a. 1.25) oil immersion objective and 15x and 20x oculars. Drawings were made with the aid of a camera lucida and reproduced at a table-top magnification of 3400x.

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OBSERVATIONS

1. *Aplysia benedicti* (Eliot): 7 individuals of this species were studied and all of them yielded good results. Seventeen bivalents could be clearly seen during diakinesis and metaphase (Fig. 1).

2. *Bursatella leachii* Blainville: 8 individuals gave satisfactory results. Fig. 2 shows 17 bivalents during diakinesis.

3. *Thordisa crosslandi* Eliot: Only 1 individual, of the 2 collected, showed dividing cells in the gonad. Thirteen bivalents could be very well discerned during diakinesis (Fig. 3).

4. *Pleurobranchaea* sp.: Only 1 individual of this species collected in September, 1968 provided the material for the present study. During diakinesis and metaphase, 13 bivalents could be clearly seen (Fig. 4).

5. *Hydatina velum* (Gmelin): 4 individuals were used in the present study and in all of them 15 bivalents were seen during the meiotic division (Fig. 5).

6. *Haminoea crocata* Pease: The 4 individuals on which it was possible to make satisfactory observations all showed 17 bivalents during diakinesis (Fig. 6).

7. *Cryptophthalmus olivaceous* Ehrenberg: 2 specimens had dividing cells which were satisfactory for study. In both specimens 18 bivalents could be clearly seen (Fig. 7).

DISCUSSION

The chromosomes of 7 genera of opisthobranchiate mollusks studied here adds to previous knowledge, bringing the number now critically studied to 85 species (in 31 families and 7 orders). Cytological information is presented for the first

FIGS. 1–7. Male diakinesis chromosomes of some opisthobranchiate gastropods from Porto Novo. X2210. FIG. 1. *Aplysia benedicti*. FIG. 2. *Bursatella leachii*. FIG. 3. *Thordisa crosslandi*. FIG. 4. *Pleurobranchaea* sp. FIG. 5. *Hydatina velum*. FIG. 6. *Haminoea crocata*. FIG. 7. *Cryptophthalmus olivaceous*.

TABLE 1. Chromosome numbers in opisthobranchs*

Family	Haploid chromosome number	Number of species studied	Locality
Notaspidea:			
Pleurobranchidae	12, 13	3	Japan, Italy, India
Nudibranchia:			
(16 families)	13	45	Japan, Marshall Is., India, Italy
Entomotaeniata:			
Pyramidellidae	17	1	Japan
Anaspidea:			
Aplysiidae	17	6	Japan, India, Marshall Is.
Cephalaspidea:			
Hydatinidae	15	1	India
Acteonidae	17	1	Japan
Philinidae	17	2	Japan, Italy
Aglajidae	17	3	Japan, Italy
Atyidae	17	3	Marshall Is., India
Smaragdinellidae	18	3	Marshall Is., India
Sacoglossa:			
Elysiidae	17	2	Japan, Italy
Stiligeridae	17	7	Japan, Italy
Juliidae	17	1	Japan
Polybranchiidae	7, 17	2	Italy
Soleolifera:			
(2 families)	16 - 18	5	Marshall Is., Japan, U. S. A., India

*From Burch (1965, 1967), Burch & Natarajan (1967), Inaba (1959, 1961), Inaba & Saiki (1967), Mancino & Sordi (1964, 1965), Natarajan (1959, 1960), and Patterson (1969).

time on the family Hydatinidae. Table 1 summarizes all currently available information, and shows the range of haploid chromosome numbers in opisthobranchs to vary from 12 to 18, with only one known exception, the sacoglossan *Bosellia mimetica* (n=7), a cytologically aberrant species (Mancino & Sordi, 1964).

All of the 45 species of Nudibranchia studied have the haploid chromosome number 13; this order exhibits an extreme case of cytological conservatism.

Two members of the notaspidean family Pleurobranchidae have been studied previously (Inaba, 1959; Mancino & Sordi, 1965); *Pleurobranchaea novaezealandica* from Japan and *P. meckeli* from Italy both have 12 pairs of chromosomes. The present study shows that another member of this family (from India) has the haploid number 13. It would be interesting to determine the chromosome numbers of other members of this family.

The haploid chromosome number 17 has been reported to occur in 29 (of the 36 studied) species of Entomotaeniata, Cephalaspidea, Anaspidea, Soleolifera and Sacoglossa, which again demonstrates the cytological conservatism which generally occurs in the Opisthobranchia. The haploid chromosome number 18, the basic number for the Basommatophora, has been found in 2 members of the Soleolifera and in all 3 species of the Smaragdinellidae (Cephalaspidea) studied. The occurrence of n=18 in the latter family led to the suggestion previously that perhaps the Basommatophora were derived from a taxon related to this cephalaspidean family (Burch & Natarajan, 1967).

The haploid chromosome number 15 now reported in *Hydatina velum* is the first chromosome number reported for a member of the family Hydatinidae, and it is also the first time this number has been reported for any opisthobranch. This helps bridge the gap in chromosome numbers that was thought to exist from previous studies, i.e., n=13 in Nudibranchia and n=17 and 18 in other opisthobranchs. Inaba (1961), while discussing the phylogeny of opisthobranchs from a cytological viewpoint, commented on this gap between the 2 most prevalent opisthobranch chromosome numbers, and mentioned that this gap raised many questions. The Hydatinidae are grouped together with the Acteonidae and Ringiculidae to form the superfamily Acteonacea (Taylor & Sohl, 1962), which are considered to be the most primitive members of the Opisthobranchia (Fretter & Graham, 1962). While other members of the Acteonacea have been found to have a haploid chromosome number of 17, *H. velum* has n=15, and thus from a cytological point of view the family Hydatinidae might be considered the more primitive. Therefore, an extensive cytological-morphological study of the Hydatinidae is desirable.

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MORPHOLOGICAL AND CYTOLOGICAL STUDIES OF THE SUCCINEID GENUS *QUICKIA* FROM INDIA[1]

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ABSTRACT

The succineid genus *Quickia* is reported for the first time in India. Based on these specimens, the diagnosis of the genus has been modified. Additionally, a new subgenus (*Burchella*) and a new species (*Q.* (*B.*) *calcuttensis*) are described. *Quickia*, which is probably represented by several species in India, was previously reported from Africa, its off-shore islands and some islands in the Indian Ocean. Morphological features of the shell, jaw, radula and the reproductive anatomy, as well as the chromosome number, are described for *Q. bensoni* and *Q. calcuttensis*. Both Indian species of *Quickia* have 25 pairs of chromosomes, the same number previously reported for *Q. spurca* from Liberia.

INTRODUCTION

Members of the land snail family Succineidae are encountered rather frequently in both terrestrial and amphibious habitats in India. Because of their extremely varied morphological features and ecological habitats, the Indian Succineidae should be of special interest to land snail systematists. Nevertheless, studies on Indian succineids are few. Amin-ud-Din (1921) described the anatomy of 4 succineid species from India. H. S. Rao (1924, 1925) is the only investigator who made a serious attempt to provide a concrete basis for a meaningful understanding of the taxonomy and systematic relationships of the various Indian succineid species. Since the publication of his 1924 study, the Indian Succineidae have received no attention, other than a brief account of the anatomy of *Indosuccinea* by Odhner (1950). I have recently had the opportunity to collect various Indian Succineidae and study some of their morphological and cytological features. This report adds to the morphological and systematic knowledge of the Indian Succineidae, and presents the first chromosome number determinations for this family from that country.

MATERIALS AND METHODS

Quickia (*Quickia*) *bensoni* was obtained from leaf litter on the ground adjacent to and from the stone wall of an empty moat at Fort William, Calcutta (June, 1969). The specimens were found at the same locality Rao (1924) collected them in July, 1923. *Q.* (*Burchella*) *calcuttensis* was collected from emergent aquatic plants at the edge of Ballygunge Lake, Calcutta (June, 1969).

Snails used for anatomical studies were anesthetized by drowning in tap water to which some menthol crystals were added. The animals gave no reaction to tactile stimuli after approximately 6 hours of anesthetization. In the hot Indian climate of June, this period was shorter by 8 hours than for the same species under laboratory temperatures of 72-75° F in Ann Arbor, Michigan. After anesthetization was complete, the snails were killed and fixed in alcohol-formalin-acetic acid (AFA or Lav-

[1]Supported by research grant SFC-7427 from the Smithsonian Institution, Washington, D. C., and Training Grant 5 T1 AI 41 from the National Institute of Allergy and Infectious Diseases, U.S. Public Health Service.

dowsky's mixture)[2] for 15 minutes and rinsed and preserved in 70% ethanol. Dissections were made in 70% ethanol using watchmaker's forceps and iridectomy scissors. A Wild M5 stereoscopic microscope equipped with a camera lucida was used during dissections and for making drawings.

Animals were fixed for cytological studies in both Newcomer's (1953) fluid and a mixture of 95% ethanol and glacial acetic acid (3: 1 parts by volume). Acetic-orcein chromosome squash preparations were made within a few hours of collection and fixation. Meiotic chromosomes were observed from field collected specimens of both species while the mitotic chromosomes of *Q. calcuttensis* were studied in a specimen from the 3rd generation of laboratory-reared snails. The snails were cultured according to the method given in Patterson (1969). Chromosomes were observed using a Leitz compound microscope fitted with 10X or 15X oculars and a 100X (n.a. 1.30) phase contrast oil immersion objective. Chromosome drawings were made with the aid of a camera lucida and reproduced at a table top magnification of 6800X. Photomicrographs were taken using a Wild compound microscope with phase contrast oil immersion objective (n.a. 1.25) and fitted with a Leitz Aristophot photomicrographic attachment and Polaroid film holder[3] using Polaroid film type 57 (3000 speed).

RESULTS

Quickia (*Quickia*) *bensoni* (Pfeiffer)

Shell

Shells of adult specimens are generally 8 to 9 mm high and 5 to 6 mm wide and have 3 whorls. Many of the live specimens collected were young adults of somewhat smaller size but 1 large adult shell 11 mm high and 6.5 mm wide was found at the collecting site. Fig. 2a, b shows the 2 extremes of shell shape represented in the Fort William population. The more ovate form is most common. In their natural state, the delicate shells of this species are usually covered with a thin layer of mud. This mud was deposited in a spiral arrangement of 3 prominent longitudinal ribs on the body whorl of some of the younger (3-4 mm) specimens, while no definite arrangement was discernible on others. The presence of the mud on the shell provided an excellent camouflage, making the specimens difficult to see at first glance. After removing the mud, the shell appears light gray-brown in color, regularly and finely striate with a straight outer lip. There is a moderately distinct columellar plait with a very slight fold. The whorls have a rounded periphery with moderately impressed sutures. Removal of the periostracum renders the shell a translucent silvery-white color (Fig. 1).

The shell of *"Succinea" bensoni* was described by Pfeiffer (1849) as ovate, conical, narrow, regularly striated, translucent, mud-colored, 3 whorls, penultimate whorl slightly convex, body whorl 2/3 shell length, columella slightly receding, aperture oval, delicate, slightly curved to the right.[4]

The shells of the specimens used in this study generally fit Pfeiffer's original description for specimens from Moradabad. The more attenuate forms from the Fort William population (see Fig. 2b) resemble the illustration for *"Succinea" bensoni* in Hanley & Theobald (1876, pl. 67, fig. 9). Rao (1924) did not give a shell description of his specimens of *"Succinea" bensoni* from Fort William.

The shells of *Quickia bensoni* from India and *Q. spurca* from Liberia are not significantly different. In fact, there are several striking similarities between the 2 forms: (1) They are of similar shape; (2) spiral mud ribs are deposited on

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[2]Composed of 50 ml 95% ethanol, 40 ml distilled water, 10 ml formaldehyde solution and 2 ml glacial acetic acid.

[3]Provided by a grant from the National Science Foundation, GB-8212 to the Museum of Zoology, The University of Michigan, for research in systematic and evolutionary biology.

[4]Translated from the latin description.

FIG. 1. Shell of adult *Quickia bensoni*. FIG. 2. Extreme shell shapes of *Quickia bensoni;* (a) ovate, (b) ovate-attenuate.

the shells of some specimens of both species and mud is commonly found on all specimens; (3) the striae are similar in fineness and regularity; (4) both are translucent white after removal of the periostracum; and (5) both species show a considerable amount of variation in shell shape.

Jaw

Fig. 3 shows an illustration of the jaw from a young adult *Quickia bensoni* from Fort William. The jaw is nearly the same in height and width when measured at the greatest dimensions. The anterior margin is slightly depressed and without a median prominence. The posterior margin of the basal accessory plate is nearly straight with rounded corners. The jaw is amber with light brown areas on the cutting piece and basal plate. The jaw of *Q. bensoni* is somewhat different from that of *Q. spurca* in that in the latter species the anterior margin is very depressed and has a median prominence (Fig. 4).

Radula

The most prevalent radular formula for *Quickia bensoni* is 14-15: 9-10:1:9-10: 14-15 in the Fort William population. There is a gradual transition from lateral to marginal teeth. This is due to the fact that the small outer cusp of the lateral does not become suddenly completely divided into 2 cusps. The number of teeth per row varied widely from 37 to 49 in the specimens examined.

Rao (1924) gave the radular formula 4:15:1:15:4 for *Quickia bensoni*. He further stated that "There are never more than five marginals, each having one or two cusps." This statement is not verified by my studies. Furthermore, marginal teeth have as many as 5 distinct cusps, 2 being large.

Reproductive Anatomy

The bodies of alcohol-preserved specimens of *Quickia bensoni* appear translucent white with the internal organs visible, especially anteriorly. The foot of

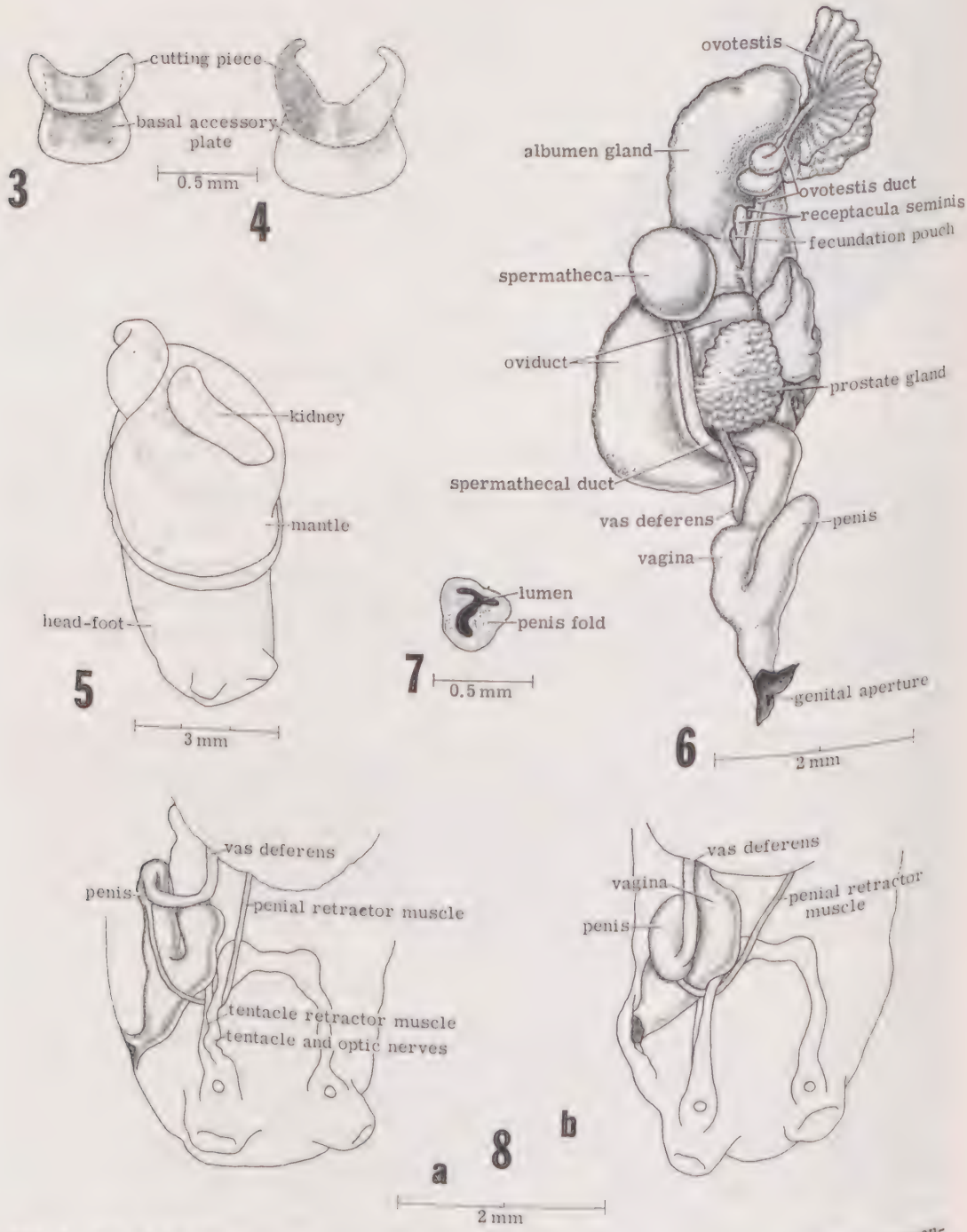


FIG. 3. Jaw of *Quickia bensoni*. FIG. 4. Jaw of *Quickia spurca*. FIG. 5. Kidney shape and pigmentation pattern in *Quickia bensoni*. FIG. 6. Ventral view of the reproductive tract of *Quickia bensoni*. FIG. 7. Cross section of the penis of *Quickia bensoni*. FIG. 8. Terminal genitalia of *Quickia bensoni*; (a) penis straight, (b) penis bent forward.

In the terminologies of various authors: ovotestis gland = hermaphroditic gland; ovotestis duct = hermaphroditic duct; seminal vesicle = mid-portion hermaphroditic duct; receptacula seminis = seminal vesicles; spermatheca = bursa copulatrix.

adult specimens measures approximately 11 mm x 4.5 mm. The kidney has the shape shown in Fig. 5 and is creamy yellow in color. Mantle pigmentation is highly variable; some specimens are quite extensively pigmented, while on others the pigmentation is minimal. Fig. 5 shows the maximum pigmentation on the mantle and head-foot region.

The ventral view of the reproductive tract of *Quickia bensoni* is shown in Fig. 6. The ovotestis is relatively large with numerous acini which are closely situated in the organ. The ovotestis is opaque-white with an occasional black pigment spot. The ovotestis (hermaphroditic gland) duct, which acts as a seminal vesicle in the distended middle portion, is lightly pigmented with black, is of moderate length and is convoluted in its mid-section. Two white receptacula seminis (previously called seminal vesicles) of slightly unequal length are evident. A well developed fecundation pouch is also present. The ducts of the ovotestis, receptacula seminis, fecundation pouch, albumen gland and vas efferens all open into or depart from the upper spermoviduct in the same region (carrefour region of other pulmonates).[5] The albumen gland is large, white and follicular. It has the usual linguiform shape. The spermoviduct is compactly folded along its length. The prostate gland is of moderate size, follicular in appearance, opaque white in color and sparsely pigmented with black. Although follicular in appearance, its structure consists of bunches of relatively small branching tubules which empty into the vas deferens, which is the usual condition in the Succineidae. The prostate is somewhat flattened. The oviduct is large with the internal folds visible externally along the lower right uteral portion. The walls of the lower oviduct become thicker and are very muscular at the point where the spermathecal duct joins, below which is the highly muscular vagina. The spermatheca is spherical in shape and opaque white in color. Its relatively long duct courses anteriorly and underneath the oviduct and enters it at a level opposite the top of the penis. Thus, the vagina is quite short in *Q. bensoni*. The vas deferens is large and courses from the prostate gland to the tip of the penis with a slight turn forming a J-configuration. The penis is approximately equal to the vagina in length, has a thick muscular wall, 2 major folds (Fig. 7), and a T-shaped lumen which is slightly visible externally under high illumination. The penial retractor muscle is long, thin and weak. It originates some distance below the tip of the penis (Fig. 8a) and inserts as a minutely thin strand in the epithelium covering a portion of the digestive tract at a level opposite the midportion of the albumen gland (ventral to and distal from the spermatheca when viewing it *in situ*). The penial retractor muscle courses underneath the tentacle retractor muscle and the tentacular and optic nerves (Fig. 8).[6] The common genital duct is quite long, has a wide lumen and muscular wall. The penis was bent forward in some specimens (Fig. 8b), but it always remained in the same orientation relative to the position of the vagina. The right tentacle assembly always passes on the inner side of the terminal reproductive tract.

In comparison to the African *Quickia spurca*, *Q. bensoni* shows several prominent differences in reproductive anatomy, such as (1) a larger ovotestis having many more acini, (2) a convoluted, pigmented ovotestis duct, (3) a prostate gland with many more smaller tubules which are more compactly organized, (4) a much

[5] The terminology used here follows the recommendations of C. J. Bayne (personal communication), and are based mainly on the function of the various structures.

[6] This condition is precisely the arrangement found in most specimens of *Q. spurca* from Liberia (see Patterson, 1968, Fig. 9b, c). However, the structure labeled tentacle retractor in the above figure is actually the tentacle assembly composed of the tentacle retractor muscle and the tentacular and optic nerves. The pigmentation is on the tissue surrounding the tentacular nerve.

shorter vagina, (5) the attachment of the penial retractor muscle below the tip of the penis (it attaches at the tip in *Q. spurca*), and (6) the penis and vagina of nearly equal length (the penis is only about 1/6 the length of the vagina in *Q. spurca*).

Chromosome Number

The haploid chromosome number of *Quickia bensoni* is n=25. Only meiotic cells were found in the field collected specimens and all snails of this species died in shipment to Michigan so that further cytological studies were not possible. The Metaphase I chromosomes are highly condensed and deeply stained (Figs. 9, 10). All chromosomes appeared to be paired as normal bivalents in all cells examined.

Quickia (*Burchella*) *calcuttensis*, n.subg., n.sp.

Shell

The shells of adult specimens have 3 whorls and range in size from 8 to 9 mm in height and 5 to 5.5 mm in width. Fig. 14 shows the shell of a young specimen collected in the field and allowed to mature in the laboratory. In their natural condition, the snails live on aquatic vegetation. The shell is generally covered with a film of water, thereby appearing very shiny and translucent. The internal organs such as the kidney, heart and digestive gland are easily visible through the shell. Upon removal of the animal, the shell appears a pale yellowish-buff in the region of the spire, and it becomes paler in the area of the body whorl until it is a translucent cream color at the apertural margin. A slight columellar fold is evident on the apertural margin of the columellar plait. This species is amphibious and does not deposit mud on its shell. The shell also has regularly spaced, fine growth striae. Variation in shell shape is minimal. The shell of *Quickia calcuttensis* is different from that of *Q. bensoni* in color, lack of appreciable variation in shape, lack of mud deposition and the presence of a noticeable columellar fold. However, it is similar in shape and striae to the more attenuate forms of *Q. bensoni*. The ecological habitats of the 2 species differ greatly.

Jaw

The chitinous jaw of *Quickia calcuttensis* is slightly higher than wide when measured at the greatest dimensions (Fig. 15). It is amber in color with gold areas on the cutting piece and basal accessory plate. The anterior margin of the cutting piece is depressed with a well-developed median prominence. The cutting piece is substantially strong and its arms are wide and rounded. The sides of the basal accessory plate are oblique inward and its posterior margin is wavy in outline. The jaw is quite different from that of *Q. bensoni* (Fig. 3).

Radula

The approximate radular formula for *Quickia calcuttensis* is 18:12:1:12:18. However, there was a variation from 55 to 61 teeth per row. The transition from lateral to marginal teeth is gradual. Marginal teeth have as many as 5 cusps with 2 of them large in size. The radula of *Q. calcuttensis* has more teeth per row than does *Q. bensoni*.

Reproductive Anatomy

The bodies of living and alcohol-preserved specimens of *Quickia calcuttensis* are slightly yellowish-translucent-cream color, with the internal organs visible

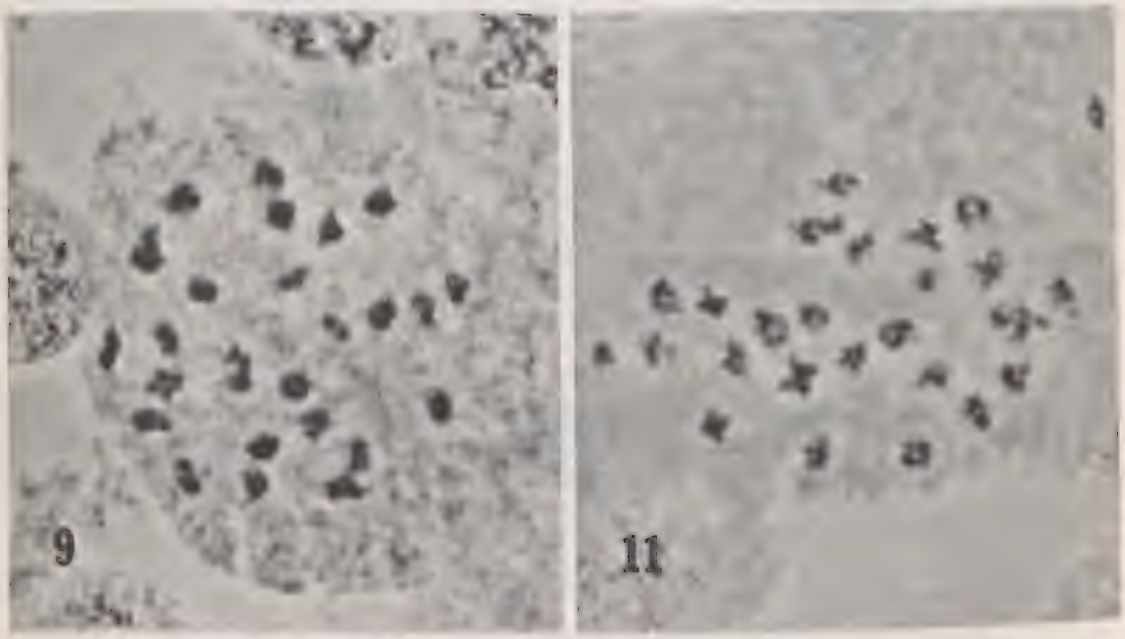
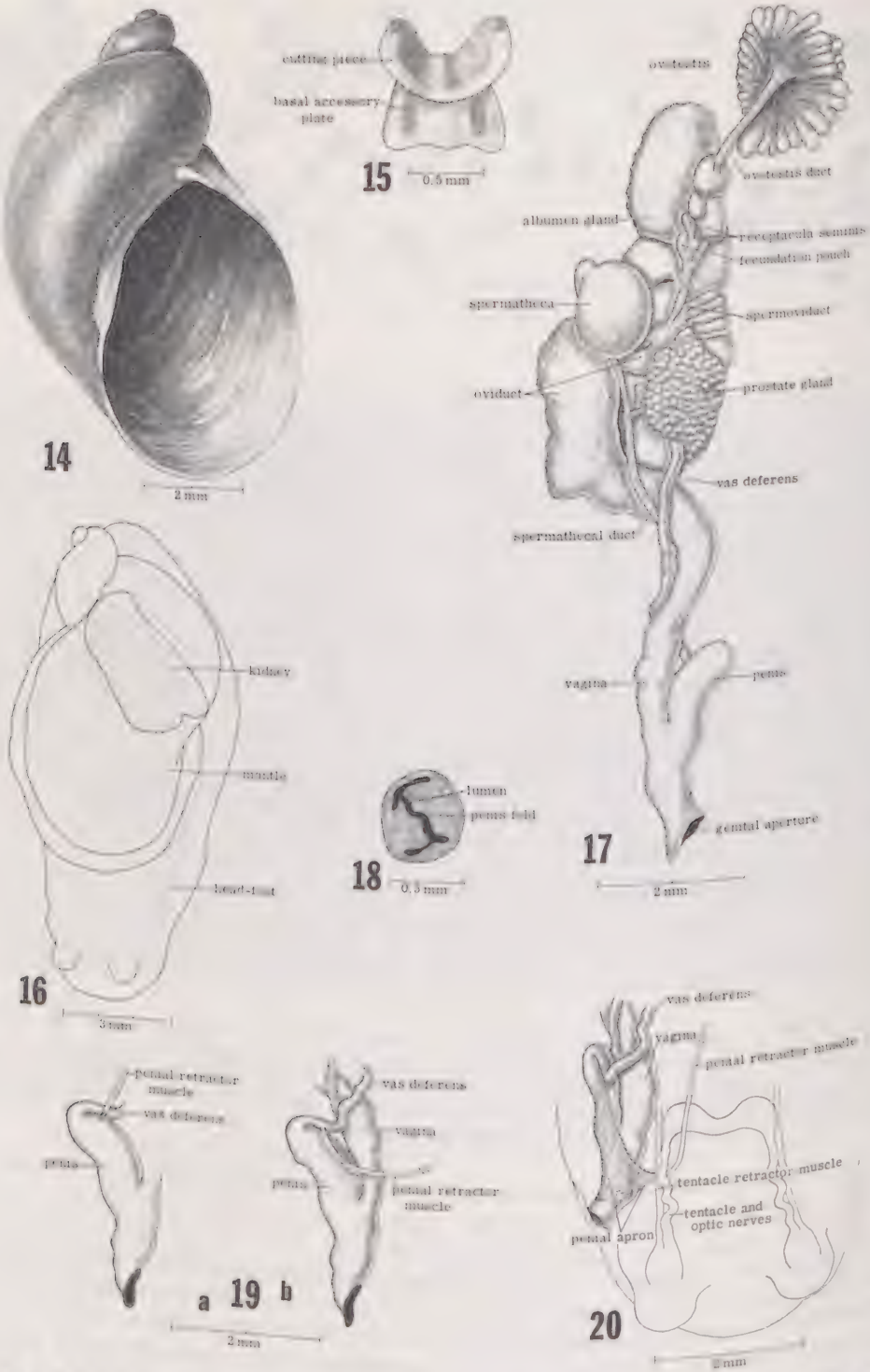


FIG. 9. Photomicrograph of late diakinesis bivalents of *Quickia bensoni* (n=25). FIG. 10. Camera lucida drawing of the late diakinesis bivalents of *Quickia bensoni* shown in Fig. 9. FIG. 11. Photomicrograph of diakinesis bivalents of *Quickia calcuttensis* (n=25). FIG. 12. Camera lucida drawing of the diakinesis bivalents of *Quickia calcuttensis* shown in Fig. 10. FIG. 13. Camera lucida drawing of a mitotic metaphase cell of *Quickia calcuttensis* (2n=50).

through the body wall. The kidney is light yellow posteriorly and becomes a light cream color at the anterior urethral margin. The kidney is somewhat bilobed on the left end. As in the other species of *Quickia*, the amount and pattern of mantle pigmentation is variable among the different individuals. The black pigmentation markings on the mantle and head-foot region of a specimen with the maximum pigmentation found is shown in Fig. 16. There is some pigmentation around the pulmonary opening. There is more pigmentation on the head-foot region in *Q. calcuttensis* than in *Q. bensoni*. Pigmentation or coloration of internal structures is discussed below.

Fig. 17 depicts the ventral view of the reproductive tract of *Quickia calcuttensis*. The ovotestis is of moderate size with large tubular acini clearly visible. There are fewer (but larger) acini than in *Q. bensoni*. The ovotestis duct is greatly



FIGS. 14-20. Morphological and anatomical features of *Quickia calcuttensis*. FIG. 14. Adult shell. FIG. 15. Jaw. FIG. 16. Kidney shape and pigmentation pattern. FIG. 17. Ventral view of the reproductive tract. FIG. 18. Cross section of the penis. FIG. 19. Penial retractor muscle, (a) with some fibers attached to penis, and (b), attachment to vas deferens which is appressed to the penis. FIG. 20. Penial apron.

distended and convoluted. Two yellow-orange receptacula seminis of subequal length and a well-developed fecundation pouch are clearly evident. Opening into the upper spermoviduct are the ducts of the ovotestis, receptacula seminis, fecundation pouch, albumen gland and vas efferens. The albumen gland is the same yellow-cream color as the ovotestis; it is follicular in appearance and linguiform in shape. The spermoviduct is compactly folded and translucent white in color. The prostate gland is white with sparse black pigmentation, although it has noticeably less pigmentation than the prostate of *Q. bensoni*. The tubules of the flattened prostate gland are similar in size and appearance to those of *Q. bensoni*, but somewhat less compactly organized. The oviduct is large with the internal folds of the lower right uteral section visible externally as in *Q. bensoni*. Anterior to that point, the thick walls of the lower oviduct become more muscular so that interior folds are not visible externally. The vagina is thick-walled, highly muscular and short as in *Q. bensoni*. The spermatheca is also an opaque yellow-cream color and is spherical in shape. Its duct courses anteriorly dorsal to the lower oviduct and joins with it at a level opposite the tip of the penis as in *Q. bensoni*. The vas deferens is longer in *Q. calcuttensis* than in *Q. bensoni*, but it extends from the prostate gland to the tip of the penis in a similar J-configuration. The penis (Fig. 18) is sheathless and highly muscular with prominent inner folds, as in *Q. bensoni* (Fig. 7). The penis is slightly longer than the vagina, and its tip lightly colored with a dull orange pigment. In *Q. calcuttensis*, the penial retractor muscle attaches on the vas deferens with fine strands extending to the penis proper (Fig. 19a). A thin connective tissue and the retractor muscle strands hold the vas deferens closely appressed to the penis from its point of origin at the penial tip to a point where the vas deferens bends upward (posteriorly) toward the prostate (a little beyond the attachment of the penial retractor muscle) (Fig. 19b). The penial retractor muscle is long, thin and delicate. It passes from the penis underneath the tentacle retractor muscle and the tentacular and optic nerves. The penial retractor muscle inserts in the thin connective tissue covering the spermoviduct on the left side at a level adjacent to the lower part of the albumen gland. A distinctive character of the subgenus *Burchella* is the presence of a well developed tissue sheet which covers the dorsal portion of the penis and part of the common genital duct (Fig. 20); this structure is here named the penial apron. The upper border of the penial apron is bounded by the penial retractor muscle. The penial nerve innervates the penial apron and in fact, the tissue of the apron is firmly attached to the penial nerve close to its point of origin at the brain. The broad attachment of the penial apron is along the outer side of the penis. In *Q. calcuttensis*, the penial apron is very well developed as a rather thick tissue sheet. It is colored with a dull orange pigment. The common genital duct is nearly equal in length to the penis and vagina. Its thick walls are highly muscular.

Quickia calcuttensis differs from *Q. bensoni* not only in possessing a penial apron, but in the following other features: (1) Some internal organs are slightly colored by a dull orange or light orange-yellow pigment; (2) the ovotestis follicles are fewer and larger; (3) the vas deferens is relatively longer; and (4) the penial retractor attaches on the vas deferens. *Q. calcuttensis* is clearly more closely related to *Q. bensoni* than to *Q. spurca*.

Chromosome Number

Quickia calcuttensis also has 25 pairs of chromosomes. A cell in late diakinesis taken from the ovotestis of a first generation laboratory-reared specimen is shown in Figs. 11, 12. The diakinetic bivalents appear as ring, single loop or cross-shaped figures with 1 or 2 chiasmata. One mitotic metaphase cell suitable for study

was found in the ovotestis of a young 3rd generation laboratory-reared individual (Fig. 13). The complete karyotype could not be determined because the positions of the centromeres of some chromosomes were not discernible. From an examination of several mitotic metaphase cells, most of the chromosomes appear to be metacentric or submetacentric. One pair of submetacentric chromosomes is conspicuously larger than the remainder of the complement.

DIAGNOSIS OF THE GENUS *QUICKIA* AND ITS SUBGENERA

Genus *Quickia* Odhner

The diagnosis of the genus *Quickia* is changed to take into consideration the characteristics of the 3 additional species now included in that genus. Shell ovate-conical, regularly and finely striate, whorls 3, aperture ovate, columellar plait present. Right tentacle retractor muscle and tentacular and optic nerves placed to the inside of the terminal reproductive apparatus. The penis possesses a penial retractor muscle, but it is without a penial sheath. Penis with or without a penial apron. Vagina long or short. Prostate gland flattened. Type species *Q. concisa* (Morelet).

Subgenus *Quickia*

Characteristics of the genus *Quickia* mentioned above. Penis without a penial apron. Named species included in this subgenus at present are *Q. concisa* (Morelet), *Q. spurca* (Gould) and *Q. bensoni* (Pfeiffer).

Subgenus *Burchella*

Characteristics of the genus *Quickia* mentioned above. Members of this subgenus differ from those of *Quickia* s.s. in possessing a penial apron. Type species *Q. calcuttensis* Patterson, (type specimen UMMZ 231086) which is the only species included in this subgenus at present. The subgenus is named in honor of J. B. Burch, Professor of Zoology, The University of Michigan.

DISCUSSION

More genera (6) of Succineidae occur in India than are known from any other country. These genera include 3 rare groups, *Camptonyx*, *Lithotis* and *Indosuccinea*. *Camptonyx* and *Lithotis* are endemic to India and appear to be restricted to a few localities in the Western Ghats. *Indosuccinea* is somewhat more widespread, occurring in various regions of India and Burma and probably "into Siam on the east and the Malay Peninsula on the south" (Rao, 1924). *Succinea* and *Quickia* are both rather widespread in India. *"Succinea" indica* would appear to belong to the genus *Oxyloma*, according to Rao's (1924) description; the terminal male genitalia possess a penial sheath and a penial appendix, which are characters of *Oxyloma*. *O. indica* is recorded from many localities in northern India (Rao, 1924; Amin-ud-Din, 1921).

Rao (1925) also described the terminal reproductive anatomy of *Succinea arboricola*. He did not mention the presence or absence of a penial sheath, but such a sheath is not shown in his illustrations. This absence, as well as the penis shape and bifurcate penial retractor muscle attachment, are characteristics shared by some species of the genus *Catinella*. But, the shortness of the vas deferens and its straight course to the prostate gland is characteristic of some *Quickia* species. Therefore, it is especially desirable to study *"S." arboricola* in greater anatomical detail in order to ascertain its proper systematic affinities. Since all *Catinella*

studied cytologically have either 5 or 6 pairs of chromosomes, and all *Quickia* known have 25 pairs, a determination of the chromosome number of *"S." arboricola* is also especially pertinent.

Currently, species of *Quickia* are known from Calcutta in the northeast to Cortallam Falls near the southern tip of India. More extensive collections will undoubtedly broaden the distribution of *Quickia* in that country. Also, several Indian species now placed in *Succinea* will probably be found to belong to *Quickia*. Two subgenera of Indian *Quickia* are recognized. It is recalled that the Liberian *Q. spurca* has a long vagina whereas both of the Indian forms have a short vagina and a radula type different from *Q. spurca*. The African *Quickia* may possibly form a subgeneric group distinct from the Indian forms.[7] However, until more African species are examined anatomically, the limits of variation in and the systematic importance of the vaginal length cannot be determined. In any case, the African and Indian species of *Quickia* seem to have experienced a considerable amount of evolutionary divergence.

The penial apron has not been recorded to exist in any succineid prior to this study. Its function is unknown but it may provide some positional stability to the penis. It is innervated by the penial nerve, as is the penial sheath of the species placed in the subfamily Succineinae. The question arises as to whether or not the penial apron represents a transitional form between the sheathless and sheathed penes found in succineids. If it is truly an intermediate form, then the validity of the 2 subfamilies, Catinellinae (lacking a penial sheath) and Succineinae (possessing a penial sheath), is questionable.

The genus *Quickia* has proven to be highly conservative with regard to chromosome number change. Since all species (from 2 continents) examined to date have 25 pairs of chromosomes (Table 1), this number of chromosomes appears to be characteristic of the genus. It will be interesting to see if other species of *Quickia* also have this same number. If they do, then chromosome number information alone would be very helpful in discerning the taxonomic position of other Indian succineids of uncertain affinity. A detailed study of morphological, anatomical and cytological features of the various Indian Succineidae is greatly needed in order to clarify their systematic relationships.

TABLE 1. Haploid chromosome numbers of *Quickia*

Species	Haploid No.	Source
Q. spurca	25	Harbel, Liberia
Q. sp.	25	South I., Aldabra
Q. calcuttensis	25	Calcutta, India
Q. bensoni	25	Calcutta, India
Q. ? *gravelyi*	25	Periyar R., S. India
Q. sp.	25	Cortallam Falls, S. India

[7] Should this be the case then *Quickia* s.s. would include *Q. concisa* and *Q. spurca* only. A new subgenus would have to be named to include *Q. bensoni* which is currently placed in *Quickia* s.s. solely on the absence of a penial apron.

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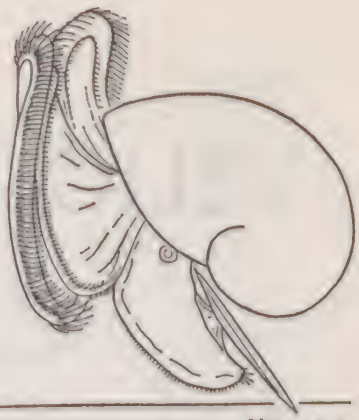

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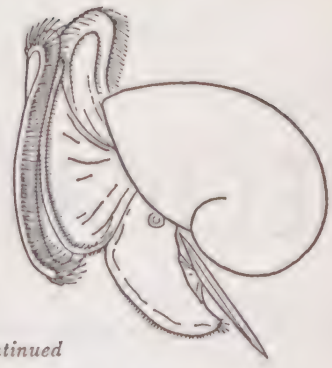

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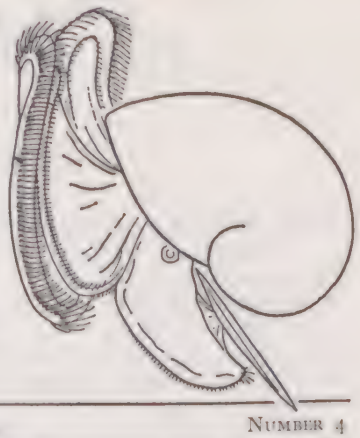

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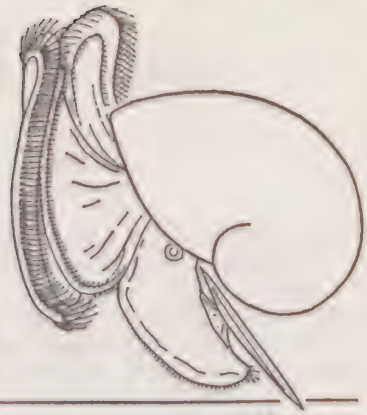

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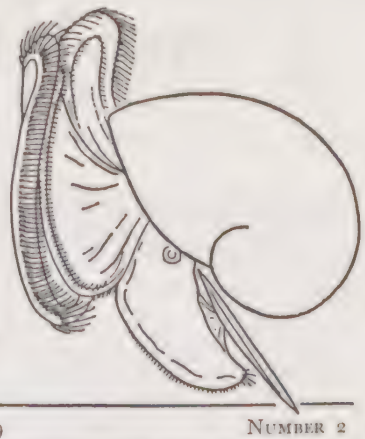

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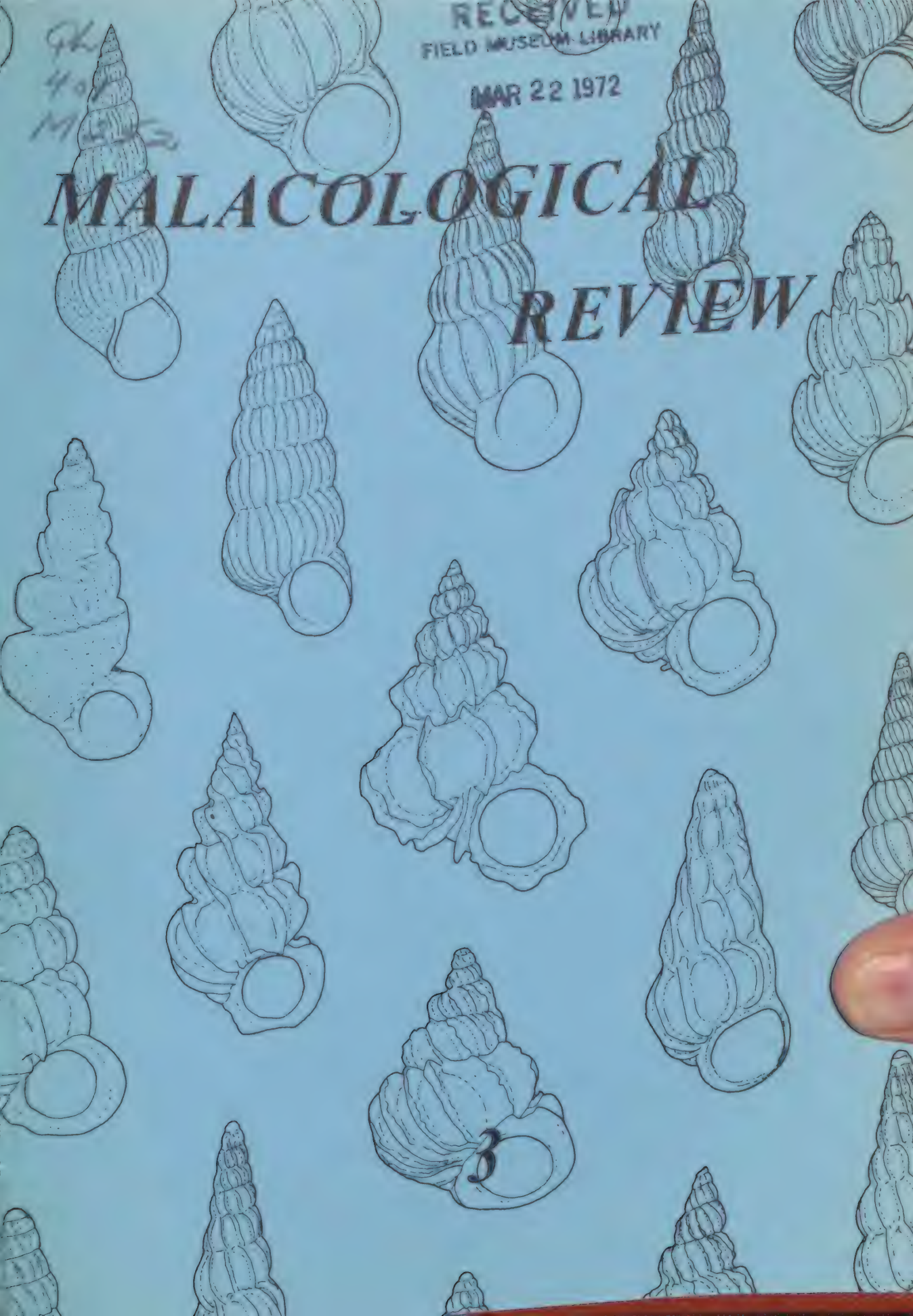

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IN VIVO REMOVAL OF BACTERIA FROM THE HEMOLYMPH OF THE LAND SNAIL *HELIX POMATIA* (PULMONATA: STYLOMMATOPHORA)[1]

C. J. Bayne and J. B. Kime[2]

ABSTRACT

The diseases of oysters and transmission of helminth parasites have been the areas of molluscan pathology receiving most attention in the past. Recently, investigations into the phylogeny of acquired immunity and into the biological significance of hemagglutinins found naturally in certain molluscan fluids have emphasized the importance of hemocytes in molluscan defense mechanisms. Our studies were undertaken to extend knowledge of these phenomena in land snails. In *Helix pomatia* Linnaeus live bacteria injected into muscle or sinuses were removed from the circulation very rapidly (within an hour). Similar bacterial injections received hours or weeks later were similarly dealt with. The injection of bacteria was followed by a rapid drop in the number of circulating hemocytes, then by an increase in their number, at least in the wounded area. No immune response was evident. Injections of colchicine or of thorium dioxide did not alter the course of changes in hemocyte numbers. The experimental technique facilitates a dynamic study of changes within the hemolymph of this snail and other species. The apparent absence of an immune response in bivalve and gastropod molluscs contrasts with the situation found in other invertebrate taxa which have been examined for such a response: oligochaetes, crustaceans, insects and sipunculids.

INTRODUCTION

Most of the available knowledge of molluscan pathology is concerned with wound-healing and certain diseases of oysters (DesVoigne & Sparks, 1968; Feng, 1966, 1967: Tripp & Kent, 1968; Alderman & Gras, 1969), or with trematode infections (Cheng, 1968). Recent reviews reflect a small but growing body of information on gastropod pathology (Pan, 1956; Michelson, 1957, 1963; Tripp, 1963; Brown, 1967; Cheng, 1967; Pauley 1969). Interest has focused on the mechanisms of defense, and it is now well established that the amoeboid blood cells (hemocytes) are most important in such defense reactions (Feng, 1967). Their ability to recognize and ingest small particles of ' non-self ' resembles this phenomenon in other phyla. The presence of hemagglutinating substances within the hemolymph and other extracts of several molluscs (Tyler, 1946; Cheng & Saunders. 1962; Boyd, Brown & Boyd, 1966; Gilbertson & Etges, 1967; McKay, Jenkin & Rowley, 1969) suggests that these substances may in some way be involved in the recognition of foreign materials by hemocytes. Recently Prowse & Tait (1969) have demonstrated the presence of opsonins within the hemolymph of *Helix aspersa*. Lysozymes active against bacteria have been reported in oyster hemolymph (McDade & Tripp, 1967).

[1]This investigation was supported in part by the United States—Japan Cooperative Medical Science Program administered by the National Institute of Allergy and Infectious Diseases of the National Institutes of Health, Department of Health, Education and Welfare, grant N.I.A.I.D. AI—07364.

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The demonstration of immune responses in arthropods (Chadwick, 1967; Acton, Evans & Bennett, 1969), annelids (Cooper, 1969) and sipunculids (Bang, 1966) has given further impetus to the search for such a response in molluscs (Weinheimer, Acton & Evans, 1969; Cheng, 1969). Despite considerable effort, however, an immune response to micro-organisms has not been clearly established, and indeed it is now fairly clear that molluscs are not capable of any humoral immune response to such organisms. On the other hand, there are suggestive data which imply a certain degree of acquired immunity to helminth parasites (Cheng, 1968), though incidentally we feel that one should not lightly dismiss the possibility that parasites within a snail may directly, by their own metabolites, reduce the likelihood of further infections. A recent report by Acton, Evans & Bennett (1969) indicates that there may be a cellular immune response capability in the oyster *Crassostrea virginica* when artificially challenged with bacteriophages.

The experiments reported in this paper were undertaken to expand our knowledge of these phenomena in the land pulmonates — Stylommatophora — utilizing the snail *Helix pomatia*. In addition to examining the rates of removal of bacteria, we also examined the possibility of an immune response.

MATERIALS AND METHODS

Adult *Helix pomatia* weighing from 12 to 18 g each were collected from Jackson County, Michigan U.S.A., in May, June and July, 1969. The snails were kept in groups of 10 at 22±2°C in clear plastic boxes, 9×6×5 inches. They were supplied with 2 inches of damp moss on the box floor, and were fed lettuce and flakes of $CaCo_3$. Fresh snails were collected several times and an attempt was made to use only snails which had been kept in the laboratory for less than 3 weeks. Each snail was used in only 1 experiment unless otherwise noted.

In all experiments the snails were injected with suspensions of a non-lethal, gram-negative bacillus previously isolated in aerobic culture from *Helix pomatia* hemolymph. The bacterium was chosen for its distinctive star-shaped colony, which allowed it to be easily distinguished from other bacteria which might be present in the hemolymph of experimental animals, and for its ability to produce a colony large enough for reliable counting after 16 hrs. growth. All culturing was done at 30±1°C in Bacto trypto-phosphate broth or on Bacto trypto-phosphate broth solidified with 1% agar.

Samples of broth cultures of the bacterium were centrifuged to form a pellet which was then resuspended in Chiarandini's (1964) physiological saline to approximately the original volume. This produced a suspension of about 1×10^8 bacteria per ml. Pre-sterilized, disposable syringes were used to inject 0·1 ml of this suspension either into the foot or into a sinus situated near the columella of the extended snail. Control snails were injected with 0·1 ml of sterile Chiarandini saline.

Injection of 0·1 ml of 0·5% Phenol Red into the foot showed that such a solution is rapidly dispersed throughout the body, the entire snail becoming pinkish within 1 minute. Thus the rapid dispersal of bacteria, evident in later results, could be effected by the circulation, even from this muscular region.

Following the injection of bacteria, samples of hemolymph were taken with capillary pipettes, made by drawing capillary tubing 1·7 mm in diameter out in a flame and breaking it to give a tip diameter (out side) of 200–300 μ. The hemolymph samples were withdrawn from the posteriorly situated columellar sinus. Pressure from the sinus could force as much as 0·1 ml of hemolymph into the pipette, but samples were generally limited to less than 0·03 ml. A sample of the hemolymph was taken within an hour before the injection of bacteria, and at several times after—usually at 15 min., 45 min., 1·5 hr., 3 hr., 5 hr. and 24 hr.

Part of the hemolymph sample was immediately blown out onto a hemocytometer and the number of blood cells present per ml of hemolymph was determined. The rest of the hemolymph was weighed to determine the volume present (specific gravity was taken to be 1), and then blown into a tube of agar medium held at 48°C. Dilutions of this tube were made to facilitate counting. The dilutions were then poured into sterile Petri plates and incubated at 30°C overnight. From the number of colonies appearing in the agar and the known amount of hemolymph in the sample, the number of viable bacteria per ml of hemolymph was calculated.

In an effort to determine whether there is in the hemolymph of fresh or pre-injected snails a soluble (humoral) factor which might inhibit the growth of bacteria, large samples (about 0·2 ml) of hemolymph were taken by opening the pericardium and allowing the hemolymph to drain into a test tube. The hemolymph was filtered through a Millipore filter (0·45 μ) to remove hemocytes, bacteria and other suspended matter. One ml of filtered hemolymph was then added to each of several tubes of agar medium at 40°C, each containing a known number of bacteria. After incubation overnight the number of colonies present was counted to see if addition of hemolymph affected the number or size of colonies.

To determine whether the injection of bacteria stimulates the production of hemocytes by cell division, 0·1 ml aqueous colchicine (0.2 mg/ml) was injected 20 minutes prior to the bacterial injection. Assuming a blood volume of 5 ml (Hyman, 1967), this produces a concentration in the hemolymph of 10^{-5}M colchicine. Hemolymph samples were taken and examined as above.

To examine the reasons behind fluctuations over time found in the number of circulating hemocytes, an attempt was made to label these cells with the radio-opaque dye Thorotrast,[a] a colloidal suspension of thorium dioxide. Brown (1967) has shown that *Helix* amoebocytes take up this material when injected. Each of 5 snails received 0·35 ml Thorotrast by injection. X-ray photographs taken 17 hrs. later showed that the snails were more opaque than controls to X-rays over their whole bodies. The normal procedure of bacterial injection and hemolymph sampling was then followed, together with X-ray photographs immediately following the bacterial injection, and at the following times after the injection of bacteria: 0·5 hr., 1 hr., 2·1 hr., 3·8 hr., 5·6 hr., 7·5 hr. and 28 hr.

It was considered that fluctuations in body weight, reported for *Helix pomatia* by Howes & Wells (1934), might possibly affect our results, so the weight cycle of *H. pomatia* was followed in our laboratory population. Whole snails were weighed daily at the same time of day for a period of 31 days.

RESULTS AND DISCUSSION

The injection of bacteria was not fatal, but immediately induced a varying degree of trauma in the snails, evident from their lack of coordination and dryer than normal body surface. The effect, when it appeared, diminished greatly within a few minutes after injection.

The results of 2 typical experiments are illustrated in Fig. 1. The injected bacteria are evident as a peak in numbers in the hemolymph samples taken within an hour of injection. The rapid and marked reduction in the number of viable bacteria was found consistently in 40 out of 42 experiments. The 2 odd cases occurred in an experiment in which rapidly repeated blood-sampling was attempted (8 samples within 30 min.), and the low number of bacteria found may be in some manner due to this difference in technique. The typical reaction followed the same course irrespective of the site of injection (foot or sinus) or of the number of bacteria injected. The dose varied from 1×10^5 to 1×10^9 bacteria per snail. Not infrequently, a rise in the number of bacteria was evident in the 3-hr. sample (e.g., Snail A. Fig. 1), and occasionally a rise in number was detected sometime during the following 14 days (e.g., Snail B, Fig. 1), but the morphology of the colonies showed that such secondary infections were not of the species injected. The very consistent finding was that the majority of injected bacteria was either rendered non-viable for plate culture or removed from the hemolymph within 1 hr. of injection. Colonies of the injected species were mostly absent from hemolymph samples taken more than 3 hrs. after the injection. This rapid disappearance of injected bacteria correlates well with the report by Prowse & Tait (1969), who studied this phenomenon in *Helix* hemocytes *in vitro*. Calculations based on data from their graphs indicate that within 1 hour the number of cells phagocytosed, expressed as a percentage

[a]From Fellows-Thestagar, 1354 W. Lafayette, Detroit, Michigan 48226, U.S.A.

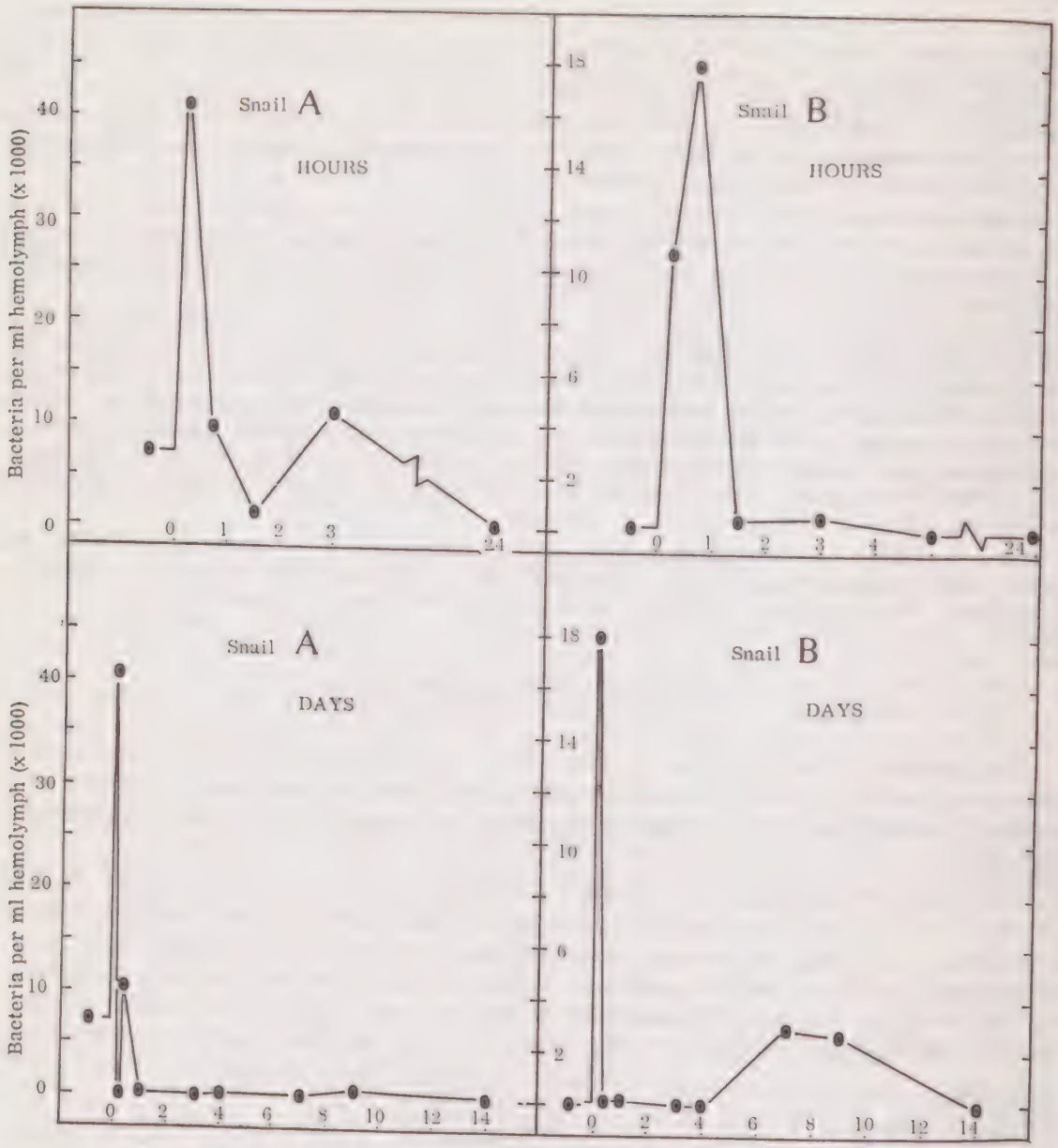
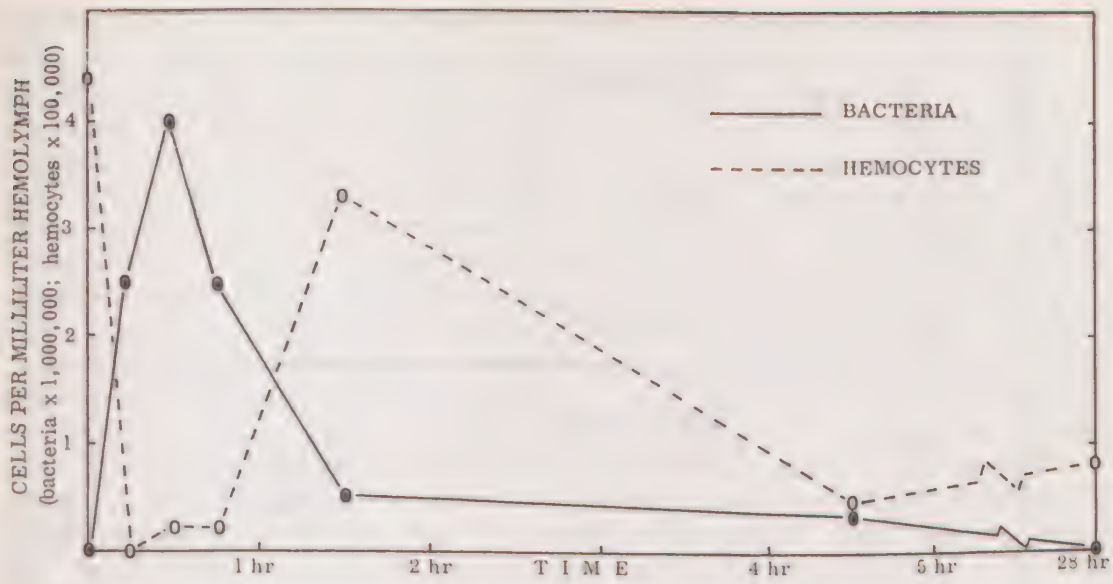


FIG. 1. Results of 2 representative experiments. Snail A received an injection of 1×10^6 bacteria into the foot tissue, and snail B received 1×10^8 bacteria into the 'columellar' sinus. The results over a short term are plotted above, and over a long term are plotted below.

of those finally phagocytosed, in their 7 reported experiments were 55, 84, 86, 64, 63, 88 and 75%.

It should be noted that there was not a consistent correlation between the known number of injected bacteria and the maximum number of bacteria per ml present in hemolymph samples taken after the injection. Representative samples are:

1×10^5 injected – – – – – – $1{\cdot}9 \times 10^4$/ml present at maximum
1×10^8 injected – – – – – – $5{\cdot}4 \times 10^6$/ml present at maximum



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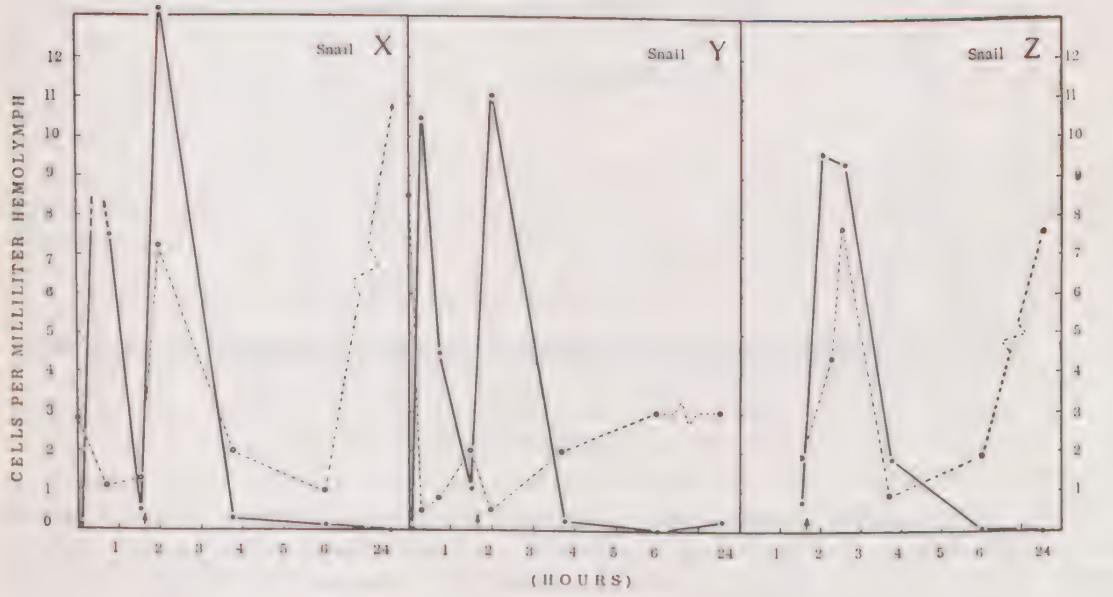

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FIG. 2. Changes in the numbers of bacteria and hemocytes in a snail which received an injection of 1×10^8 bacteria.

FIG. 3. Double injections. Three snails were each injected with 1×10^8 bacteria at t_0 and again at t+1 hr. 40 mins. *Snail X*: no 15 min. sample. Bacteria $\times 10^4$, hemocytes $\times 10^5$. *Snail Y*: bacteria and hemocytes $\times 10^5$. *Snail Z*: blood samples only after 2nd injection. Bacteria $\times 10^4$, hemocytes $\times 10^5$. Bacterial numbers follow similar courses after each of the 2 injections. Bacteria=solid lines; hemocytes=dotted lines.

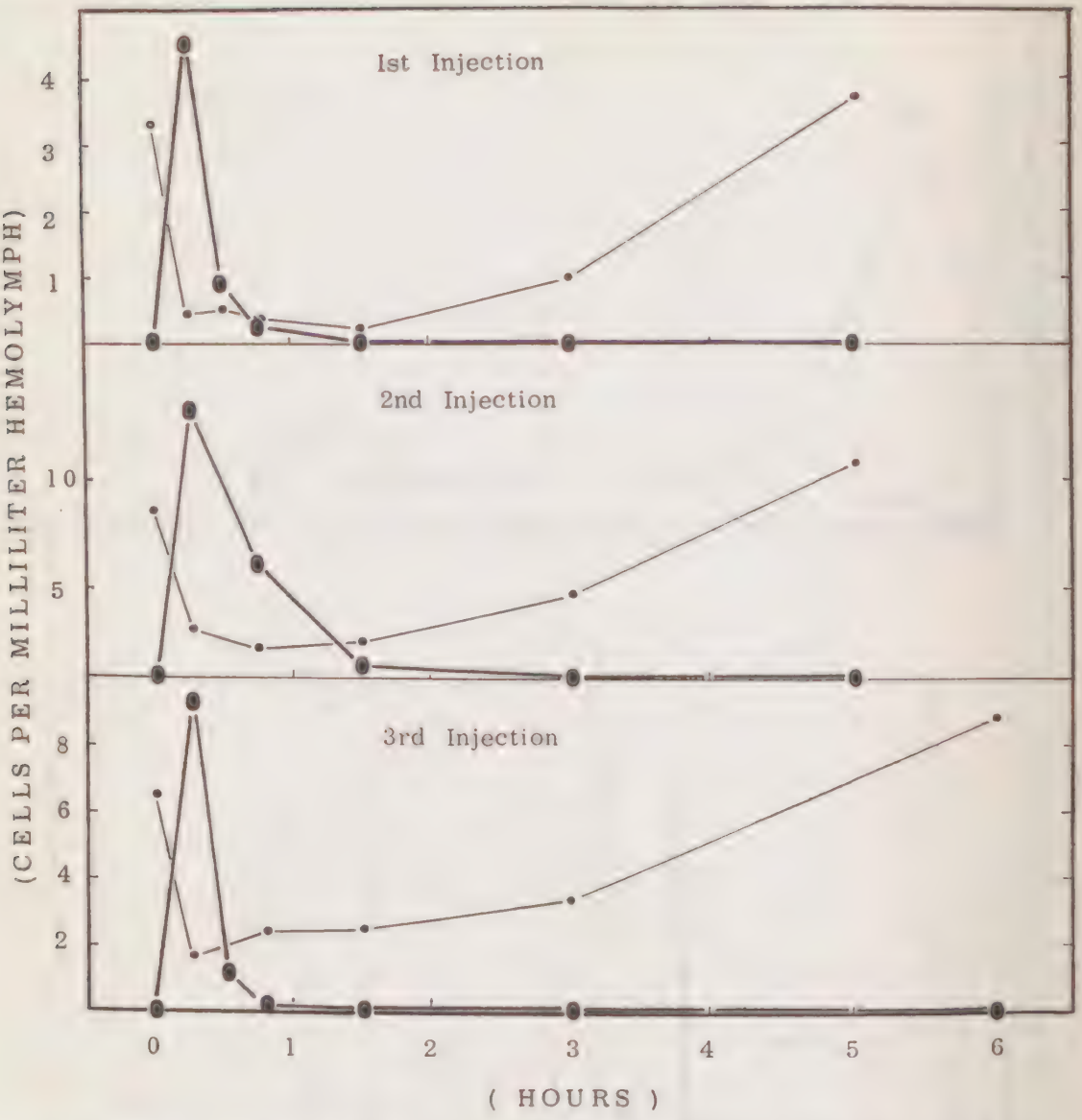

FIG. 4. Three injections in 1 snail. The 2nd injection was received 2 weeks after the 1st, and the 3rd was received 1 week later. ●——● = bacteria. ●——● = hemocytes. Note the similarity of the reaction in each case. *1st*: bacteria and hemocytes $\times 10^5$. *2nd*: bacteria $\times 10^4$, hemocytes $\times 10^5$. *3rd*: bacteria $0{\cdot}4 \times 10^5$, hemocytes $\times 10^5$.

1×10^8 injected – – – – – – $4{\cdot}5 \times 10^5$/ml present at maximum
„ injected – – – – – – $7{\cdot}5 \times 10^4$/ml present at maximum
1×10^9 injected – – – – – – $1{\cdot}4 \times 10^6$/ml present at maximum
„ injected – – – – – – $1{\cdot}0 \times 10^6$/ml present at maximum
„ injected – – – – – – $6{\cdot}4 \times 10^5$/ml present at maximum
„ injected – – – – – – $2{\cdot}9 \times 10^5$/ml present at maximum
„ injected – – – – – – $2{\cdot}0 \times 10^5$/ml present at maximum

Observations on hemocyte numbers indicated that the number of these cells in circulation before any experimental handling of the snails varied from 8×10^4 to 2×10^6 per ml; however, most snails had counts near the lower figure, the mean number being 2×10^5 hemocytes per ml of hemolymph. Following injections of bacteria the number of hemocytes normally dropped off markedly, at least in the sampling area (Fig. 2; also Figs. 3, 4 and 6), rising again after the bacterial population was lowered. In the absence of bacterial injections (control snails) the hemocyte count rose sooner and to higher levels (Fig. 6). It is likely that the changes in hemocyte numbers are reflections of 2 separate phenomena: (1) the initial drop is due to a real decrease in numbers in circulation, perhaps as a result of clumping or an increased adhesion of these cells to the walls of the circulatory system, and (2) the later increase in numbers is due to aggregation of hemocytes in the region of the injection/blood sampling wound. This later phenomenon was probably responsible for the unusual number of hemocytes seen in snails X and Z (Fig. 3) after the 2nd injection. It may also have been responsible for the absence of a peak in the concentration of bacteria in the hemolymph in the 2 odd experiments of the 42 mentioned above. In these 2 experiments the rapidly repeated blood sampling may have resulted in excessive tissue damage, attracting large numbers of hemocytes to the wound site with a subsequent local reduction in the bacterial population. The inverse relationship of bacteria to hemocytes following injection is paralleled by a similar report for the lobster (Stewart, et al., 1969).

The experiment illustrated in Fig. 3 indicates a remarkable capacity for the removal of bacteria. Each of these snails received injections of 1×10^8 bacteria twice within 1·7 hr., and after each injection were capable of reducing the number of circulating viable bacteria to very low levels within 2 or 3 hrs. The course of the reaction was similar after both the 1st and 2nd injections.

If an immune response were to develop it would probably be evident only after several days. Two snails were therefore injected on July 14, 1969, again 2 weeks later and again an additional week later. The courses of bacterial and hemocyte numbers per ml hemolymph (Fig. 4) were typical on each occasion. If an induced bactericidin were present, the number of viable bacteria in the hemolymph after the 2nd or 3rd injections would have been relatively lower. There appears to be no humoral mechanism working to reduce the numbers of viable bacteria; hemocyte phagocytosis appears to be the only defensive mechanism present, as has been concluded for other molluscs (Cheng, 1969).

Fig. 5 shows the data from 3 experiments in which the numbers of bacteria in the hemolymph were measured by both plating (culture) and hemocytometer methods. In all 3 experiments the numbers apparent from the direct hemocytometer method remained high for a longer time than numbers of resulting colonies indicated. Notably at 1·5 hr. after injection the number of bacteria measured by plating was always very low, and the numbers measured by the microscope were 10x, 1,200x and 42x higher than the number of colonies indicated. This discrepancy is certainly surprising. It would seem to indicate that there are more bacteria in circulation than are able to reproduce when "plated out"; that is, there are large numbers of non-viable bacteria present. Even if we accept the possibility of an experimental error of the order of 10x, these data still require some explanation. It seems possible that opsonins present in the hemolymph (Prowse & Tait, 1969) may reduce viability even before phagocytosis occurs, although our trial experiments (see below) did not reveal the presence of such a substance. Alternatively, there may be selective phagocytosis of vegetative bacteria until their density is reduced (about 1 hr.), after which non-vegetative cells are ingested (Tripp, 1960). Other

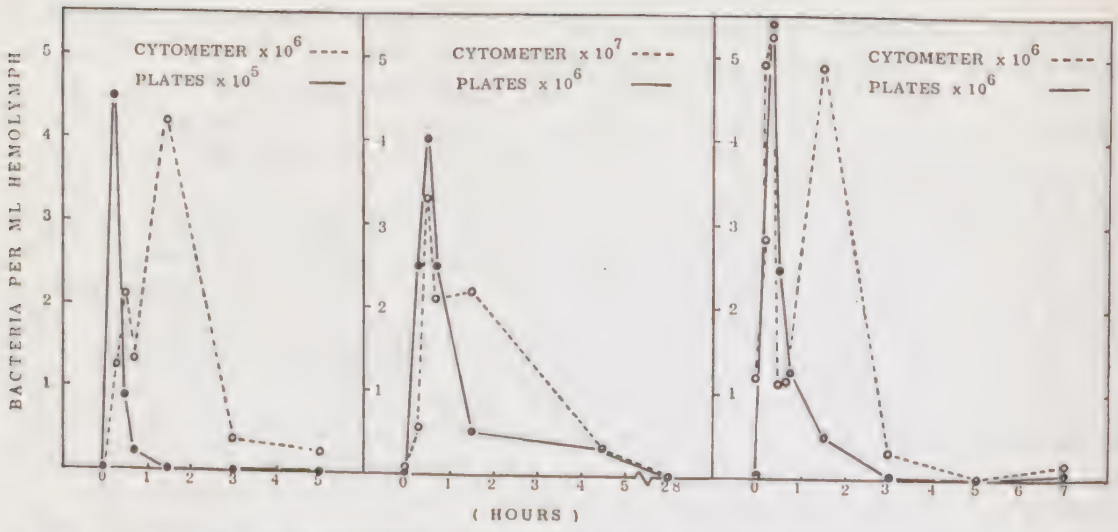

FIG. 5. Comparisoms of bacterial counts arrived at by use of a hemocytometer and by use of the agar culture-plate method.

possible explanations are to be found in the experimental technique. A cursory comparison of bacterial colonies arising from anaerobic agar culture of a streak of hemolymph revealed that there may be some bacteria present in *Helix* hemolymph which will not grow under the aerobic conditions used in this set of experiments. Furthermore, other bacteria in *Helix* hemolymph may not have found the tryptose-phosphate medium at all suitable for growth. It is also pertinent to consider the possibility that phagocytosis of bacteria may have continued within the micropipettes of hemolymph between the moment of sampling and the time when the hemolymph was blown into the culture medium. In early experiments, however, an attempt was made to plate the samples immediately after they were drawn, and there is no overall difference in the results of these experiments and those done later, in which there was often a 15-minute delay between the collection and plating of hemolymph.

The injection of colchicine 20 minutes prior to the bacterial injection (Fig. 6) did not alter the ability of the snail to increase the number of hemocytes appearing in the samples. The hemocytes thus are most probably present in the circulatory system before bacterial injection, and, as mentioned above, the apparent increase in numbers is probably due to their aggregation in the area of the wound. It was expected that the injection of thorium dioxide would be followed by its uptake by the hemocytes (Brown, 1967) so that X-ray photographs would reveal any clumping which was occurring. Unfortunately, the photographs revealed no localization of the thorium in the experimental or the control snails. The latter snails, treated identically with those of Brown (1967), did not reveal the same results as he reported. The reasons for this remain obscure. It is also pertinent that injections of bacteria did not result in a more rapid loss of opacity (=thorium dioxide). It may be, then, that the hemocytes are not destroyed or eliminated during the reduction of the bacterial population, and digestion of the micro-organisms seems likely. This contrasts with the theoretical fate of hemocytes following ingestion of colloidal Thorotrast (Brown, 1967). It is known (Tripp, 1961) that reactions of snails to injected particles vary with the nature of the particles.

Inclusion of sterile hemolymph in agar cultures of bacteria did not noticeably affect the number or size of bacterial colonies, even when the hemolymph was taken from snails

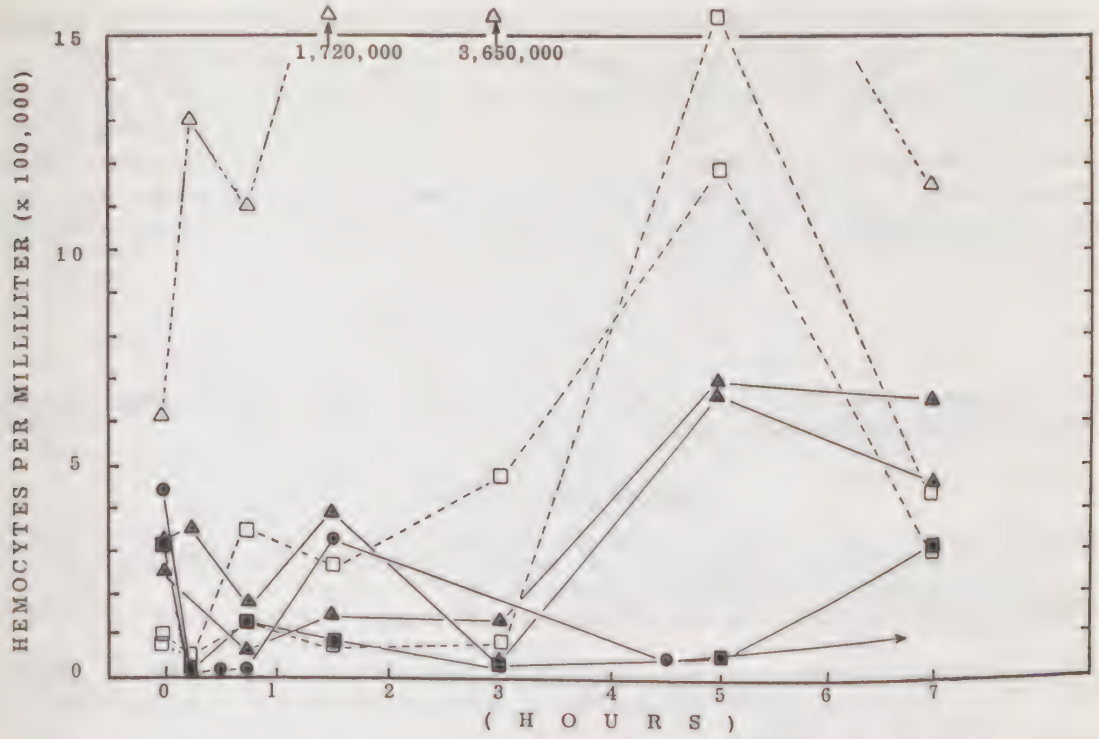

FIG. 6. Changes in the numbers of hemocytes appearing in hemolymph samples after various treatments. ●=bacteria only; ▲△=colchicine (+bacteria): ■□=thorium dioxide (+bacteria); —=bacteria; - - - - - =no bacteria.

The following points may be noted: (1) injections of colchicine or of thorium dioxide did not result in a lower hemocyte count; (2) by t+45 min. the hemocyte count is up in all snails with no bacteria, and down in all snails with bacteria; (3) bacterial injections result in a smaller number of hemocytes in the sample, most markedly over the 3–5 hr. period; (4) the high numbers around 5 hr. may reflect wound-healing activity in the area of the sample.

which had been injected with bacteria several days prior to the bleeding. The data do not, however, warrant a final statement as to the absence of a humoral factor affecting the bacteria.

The studies of weight fluctuations confirmed the report of Howes & Wells (1934). Maximum diurnal weight variations of 29% increase and 20% decrease were found. The periodicity of the weight fluctuations (several days) was much longer than the periodicity of bacterial and hemocyte variations, so that there is no danger that the results of the experiments on cell numbers may be significantly affected by variations in the volume of the hemolymph.

Investigations which have been concerned with the pathology of more than 1 species of micro-organism in invertebrates (Feng, 1966; Cheng, 1969; Johnson, 1969) have revealed that the reactions of the invertebrates quite naturally varies with the species of injected micro-organism (Feng & Stauber, 1968). It would, therefore, not be advisable to conclude that the reactions of *Helix pomatia* reported in this paper are typical in all cases of bacterial infection. The value of these experiments lies in the clarity with which they have demonstrated and given us a better understanding of an important defense mechanism in this snail. The data are compatible with results of other investigations

on the rates of removal of phages and foreign cells from molluscs (Tripp, 1961; Presnell, Cummins & Meiscier, 1967; Hamblet, et al., 1969; Acton, Evans & Bennett, 1969).

The demonstration of immune responses in the other invertebrate taxa which have been examined for this capability — annelids, insects, crustaceans and sipunculids — contrasts with the situation in the gastropod and bivalve molluscs. Here the available evidence indicates no such response, with the possible exception of phages in oysters. The cephalopod molluscs are more complex physiologically, including their circulatory system, and they should be examined for such a response.

ACKNOWLEDGEMENTS

It is with pleasure that we thank Dr. J. B. Burch for his stimulating ideas and continued encouragement, and for his generous help in acquiring research facilities.

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ADDENDUM. Subsequent experiments with injections of the bacterium *Serratia marcescens* have shown that the numbers of bacteria in the hemolymph follow a similar course to that reported in this paper (Fig. 1). Also, the numbers of viable bacteria were not reduced *in vitro* when capillary tubes with hemocytes and bacteria-laden hemolymph were incubated at 25°C in the dark for periods up to one hour.

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A NOTE ON THE CYTOLOGICAL STRUCTURE AND FUNCTION OF THE DIGESTIVE DIVERTICULA OF *MACOMA BALTHICA* CORRELATED WITH THE RHYTHM OF THE TIDE

Brian Morton[1]

ABSTRACT

Macoma balthica (Linnaeus) possesses a rhythm of digestion in the digestive diverticula which can be related to the tidal cycle, and which includes (1) the absorption in the digestive diverticula of food material derived from the sea only when the animal is covered by the tide; (2) the breakdown of the digestive tubules at low water to pass food material to the rest of the body and waste to the stomach to be voided via the anus; and (3) the reformation of old tubules and formation of new tubules at mid-tide to prepare the animal for another phase of digestion when feeding commences on the rising tide. Therefore it is concluded that *Macoma* is a rhythmical feeder like those bivalves which have recently been shown to be discontinuous feeders and whose activities are regulated by environmental variables.

The demonstration in *Macoma* of tubules which possess a wide range of structure emphasizes the need for physiologists to determine the phase of a particular structure before attributing to it a function.

INTRODUCTION

The digestive diverticula of bivalve molluscs has been investigated by Yonge (1926), Owen (1955), J. E. Morton (1956), Dinamani (1957), Sumner (1966a, b), McQuiston (1969) and B. S. Morton (1969, 1970a, b, c).

The work of J. E. Morton (1956) and McQuiston (1969) on *Lasaea rubra* and B. S. Morton (1969, 1970a, b) on *Dreissena polymorpha*, *Cardium edule* and *Anodonta cygnea* has shown that these species possess diverticula whose structure varies in accordance with a rhythm of the environment. In the case of *Dreissena* the environmental variable is day and night, and the tidal cycle in the case of *Lasaea* and *Cardium*. *Anodonta* possesses a rhythm that is apparently endogenous (Barnes, 1955).

Macoma balthica (Linnaeus) is a tidal animal living principally in the upper regions of the intertidal zone to low water (Tebble, 1966). *Macoma* is consequently a suitable animal to examine further the effect of the tidal rhythm upon the structure of the digestive diverticula. The results of this investigation are reported here.

MATERIALS AND METHODS

In the summer of 1969 large numbers of *Macoma*, obtained from Southend, England, were placed in a tidal machine, which simulated the tidal movements at Southend. A full tidal cycle lasted 12 hr. 20 min., and gave a high tide of 8 inches. When the animals were placed in the mud containers, they quickly burrowed and were in a position which simulated mid tide level on the shore. The mud used in the

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aquarium came from Southend. The temperature in the aquarium was kept at the same temperature as the sea at Southend. Artificial light was supplied during normal hours of daylight. The aquarium water was aerated and enriched at regular intervals with small quantities of cultures of marine algae.

After allowing the animals to adapt for 2 weeks to life in the tide machine, specimens were removed at hourly intervals over a full tidal cycle and fixed in alcoholic Bouin Duboscq. The tissues were sectioned at 6–8 μ and then stained in either Heidenhain's Haematoxylin and Light Green or Heidenhain's Azan. The experiment was repeated on 2 further occasions.

Full credit for the greater part of the design and construction of the tide machine used in these experiments is gladly given to Mr. J. Baylie and Mr. N. A. Thorpe of the Department of Zoology, Chelsea College of Science and Technology.

RESULTS

The cytological appearance of the digestive diverticula as seen in these preparations was found to be more or less constant in any one animal, but to differ in different specimens. The structure of the primary and secondary ducts was essentially as described for many other bivalves by Owen (1955). The structure of the digestive tubules can be interpreted as successive stages in a cyclical rhythm correlated with the rhythm of the tide (Fig. 1).

The digestive tubules of bivalve molluscs have been shown to be composed of 2 types of cells: (1) the digestive cell and (2) the basiphil cell (Sumner, 1966a, b) or the synonymous " young cell " of Yonge (1926). In *Macoma* the same 2 cell types can be distinguished, the basiphil cells lying in groups in the crypts of the tubule and separating larger groups of digestive cells. The number of groups of basiphil cells in *Macoma* is characteristically 3. The basiphil cells stain much darker than the digestive cells in Heidenhain's Haematoxylin and are consequently easy to recognise.

Three hours after high tide, the digestive tubules have the characteristic structure seen in bivalves, which can be compared to the structure of other bivalve tubules described by Owen (1955), Dinamani (1957) and Yonge (1926). The basiphil cells are orientated toward the lumina of the tubules, and the digestive cells are swollen and possess many food vacuoles (Fig. 1, A). An hour later the digestive cells show the first stages of breakdown, the vacuoles moving towards the base of the cell and apparently fusing to form larger vacuoles (B). Two hours before low tide, the digestive cells have almost completed the process of breakdown, the vacuoles have formed large " fragmentation spherules ", which according to Owen (1955) subsequently pass into the stomach where they may fragment and assist primary extra-cellular digestion by the release of enzymes. This is the basis for extra-cellular digestion in the stomach of *Lasaea* (J. E. Morton, 1956). The basiphil cells have lost their orientation toward the lumen of the tubule, and some lie in clusters still within the confines of the basement membrane of the tubule (C). At low tide most of the cell nuclei have apparently left the tubule, and all that remains is a basement membrane with only 1 or 2 nuclei lying on it (D. E). Small clusters of cells in the haemocoel (M) are, it is postulated, groups of basiphil cells which will eventually develop a lumen (N) and eventually form a new tubule. It is probable that the connection between the cluster of cells and parent tubule is not lost and that a lumen develops to connect the two. After low tide the basement membrane has apparently been repopulated by cells (F) and these cells, which are extremely short, form a lining on the internal surface of the basement membrane. Both digestive and basiphil cells can be recognised. Three hours before high tide the cells have grown, the basiphil cells form the characteristic crypt and the digestive cells have swollen with a corresponding diminution of the lumen of the tubule (H). One hour before high tide (I) and at high tide the digestive cells have

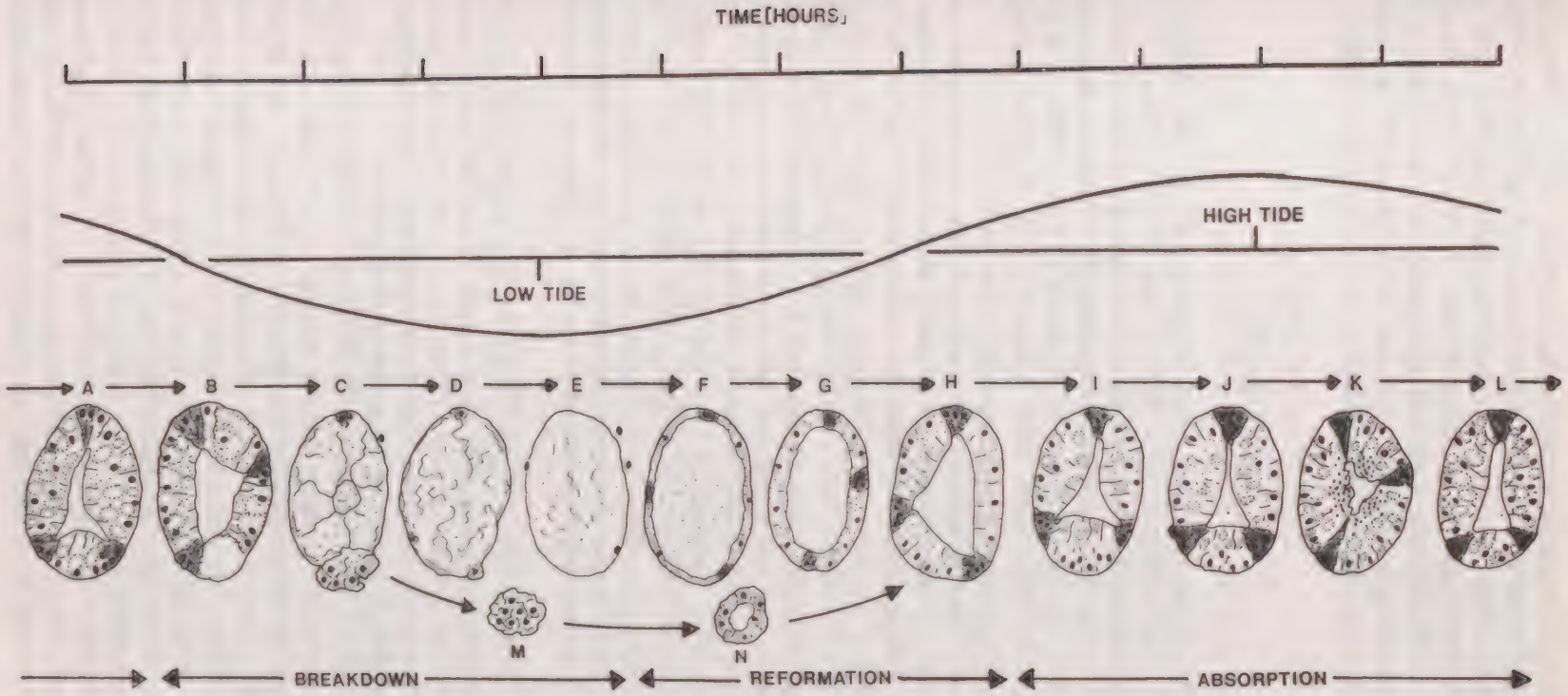

Fig. 1. A correlation between the tidal cycle and sequence of cytological changes in the digestive diverticula of *Macoma balthica*. For the stages A–N see text.

swollen even further and characteristically possess a brush border. The digestive cells have also developed food vacuoles in the distal portion of the cell (J). One hour after high tide large numbers of particles, approximately 1μ in diameter, had been phagocytosed by the digestive cells (K) which had swollen yet further. Two to 3 hours after high tide (L, A) the vacuoles in the digestive cells had apparently moved towards the base of the swell and fused to form larger vacuoles. Return to this phase (A) prepares the animal for another cycle of events and another phase of absorption and digestion in the next tidal cycle.

DISCUSSION

A variety of physiological functions have been ascribed to the digestive diverticula of bivalve molluscs. List (1902), Vonk (1904), Yonge (1926), Owen (1955) and B. S. Morton (1969) showed that the digestive cells are capable of phagocytosing particles of such substances as Indian ink, carmine, iron saccharate, titanium dioxide and colloidal graphite respectively. With the exception of Mansour & Zaki (1946), it is now generally agreed that the digestive cells ingest food material for intra-cellular digestion. This view is supported by this series of experiments upon *Macoma*.

The darkly staining or basiphil cells have been the subject of much controversy, Yonge (1926) and B. S. Morton (1969, 1970a, b, c) believing them to be generative, McQuiston (1969) and Sumner (1966b) believing them to be secretory. For some species, e.g., *Astarte* (Saleuddin, 1965), *Dreissena* (B. S. Morton, 1969), *Cardium* (B. S. Morton, 1970a) and *Aloidis*, *Ostrea* and *Venerupis* (Owen, 1955) cilia have been shown to arise from the basiphil cells. McQuiston (1969) has shown that the darkly staining cells of the tubules of *Lasaea* are secretory and not generative, the latter function being ascribed to non-secretory terminal cells of the tubule, which he postulates gives rise to both types of digestive and basiphil cells. *Macoma* is very like *Lasaea* in that the breakdown of the tubules (Fig. 3) is total and it may well be that similar terminal cells are responsible for the repopulation of the tubule. This similarity does not however explain how new tubules are formed, nor can it explain the disorientation of the nuclei of the basiphil cells to form the clusters of cells observed in *Macoma* and in earlier studies upon *Dreissena*, *Cardium* and *Anodonta*.

It may well be that terminal cells do replace digestive and basiphil cells after breakdown, but the basiphil cells themselves can only be assumed to be highly specialised, fulfilling a number of functions in different genera. They may be secretory, possess flagella, or be generative, and it may yet be shown that these cells fulfil these functions within the spatial confines of a cyclically occurring sequence of events.

Brafield & Newell (1961) have suggested that *Macoma* behaves as a suspension feeder when covered by the tide and confines deposit feeding to low water. From this study it has been shown that food is absorbed in the digestive diverticula *only* when the animal is covered by the tide. During low tide the tubules are passing digested material to the rest of the body, voiding waste material in fragmentation spherules and preparing the tubules for another phase of absorption. It would appear therefore that *Macoma* is probably only a filter-feeder and that deposit feeding, if it occurs, plays little or no part in the nutrition of the animal.

The present investigation of the structure and function of the digestive diverticula of *Macoma* shows that this animal is not a continuous feeder, and that the processes of feeding and digestion are rhythmic and can be correlated with the rhythm of the tide.

B. S. Morton (1969, 1970a, b) has suggested that a change in scientific thought is called for regarding the feeding habits of bivalve molluscs. The present investigation not only supports this view that bivalve molluscs are discontinuous feeders, but also shows that future studies on the function of the digestive diverticula must take into account the fact that the structure of the diverticula changes in accordance with a rhythm of the environment. That this controlling factor varies from species to species is expected in a group which has adapted to life in most aquatic habitats.

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INFECTION OF DIPLOID *BULINUS* s.s. WITH *SCHISTOSOMA HAEMATOBIUM*[1]

C. T. Lo[2], J. B. Burch[3] and C. H. J. Schutte[4]

ABSTRACT

Two populations of diploid South African *Bulinus* s.s. have been infected with strains of *Schistosoma haematobium*. This confirms the previous reports by Pitchford & Schutte on one of the populations (which they could not identify as to precise original locality), and extends susceptibility data to a population of known indigenous origin (Lake Sibayi). Our cytological observations and immunological tests show that these 2 populations belong to the usually refractory diploid *B. tropicus* species group, and not to the more northern generally susceptible polyploid *B. truncatus* group, in spite of several morphological similarities (shape of radular mesocones and shell shape) to the latter. These observations indicate that the diploid ancestor of the *truncatus* group was probably a snail similar to these susceptible diploid populations.

INTRODUCTION

Members of the *Bulinus tropicus* species group which occur south of the Sahara have been traditionally considered to be refractory to infection with *Schistosoma haematobium*. More recently, in our own laboratory, Lo (1968) was also unable to infect any species of this group, i.e., diploid *Bulinus* s.s.[5] (with the haploid chromosome number n=18) with the Egyptian strain of this parasite. However, Pitchford (1965) and Schutte (1966) reported that a South African *Bulinus* s.s. population (referred to the *B. truncatus* species group) had been infected with South African strains of *S. haematobium* and *S. mattheei*, as well as Iranian strains of *S. haematobium* and *S. bovis*. Therefore, we were quite anxious to test the susceptibility of descendants of Dr. Pitchford's population, as well as another South African population of *B. natalensis* available to us. It is on the results of these studies that this report is based.

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[4]Contribution published by permissoin of the South African Council for Scientific and Industrial Research.

[5]The traditional " subgenus " *Bulinus* s.s. corresponds to the present day *tropicus* (incl. *natalensis*) and *truncatus* species groups. The species group concept in *Bulinus*, replacing the subgeneric divisions, was subsequently established to avoid a nomenclatorial impasse. Strict adherence to the rules would have involved replacement of the well known name *Bulinus* for important vectors in this subgenus by the available name *Isidora*. Nevertheless the old subgeneric division facilitates the exposition of relationships and is here maintained for convenience.

FIG. 1. Photographs of typical shells of lab-raised specimens of our *Bulinus* populations from (*a*) Nelspruit, and (*b*) Lake Sibayi. The shell in (*a*) is 7 mm in height, that in (*b*) is 6 mm high. Each are true-breeding forms, exhibiting little variation in laboratory stocks. Brown (pers. comm.) considers the Lake Sibayi specimens to conform to the nominal species *B. zuluensis* Melvill & Ponsonby, which he regards as a synonym of *B. natalensis* Küster.

MATERIALS AND METHODS

Infectivity studies. The *Bulinus* s.s. specimens used in these studies were all laboratory-raised, 2–4 mm (shell height) in size. They came from 2 localities: (1) Outdoor aquaria at the Nelspruit laboratory of the Council for Scientific and Industrial Research, Transvaal, South Africa (Fig. 1a) and (2) Lake Sibayi, Zululand, South Africa (Fig. 1b). The Nelspruit snails are high-spired, similar to Krauss' (1848) *B. tropicus* and the Lake Sibayi specimens are low-spired like Küster's (1841) and Krauss' (1848) *B. natalensis*. Snails of these 2 populations were exposed to miracidia of 3 strains of *Schistosoma haematobium*: (1) an Egyptian strain originally established in 1956 by E. G. Berry at the Laboratory of Parasitic Diseases, U.S. National Institutes of Health, and transferred to our laboratory in 1965; (2) an Iranian strain obtained in 1966 from J. Massoud in Dezful, Iran; and (3) a Rhodesian strain obtained in 1968 from L. Husting in Salisbury, Rhodesia.

Eggs of each parasite were obtained by grinding infected intestines of hamsters. The eggs were concentrated by settling in cold water (10–15°C) and were hatched in warm water (30°C). Snails were exposed *en masse* at 24–26°C (room temperature) to an average of 20 miracidia each in 4 ml. of water per snail. All miracidia were less than 3 hrs. old. Only spring water was used in these experiments.

Determination of chromosome numbers. Chromosome numbers of our specimens were determined from acetic-orcein squashes of ovotestis tissues of the actual infected and non-infected snails, and from those snails from which foot muscle was taken to supply antigen for the immunological tests. These cytological procedures were the same as those used in this laboratory in previous studies with *Bulinus* (e.g., see Burch, 1964). Chromosome counts were most generally made from male diakinesis cells, although satisfactory Metaphase I and spermatogonial cells were also carefully observed.

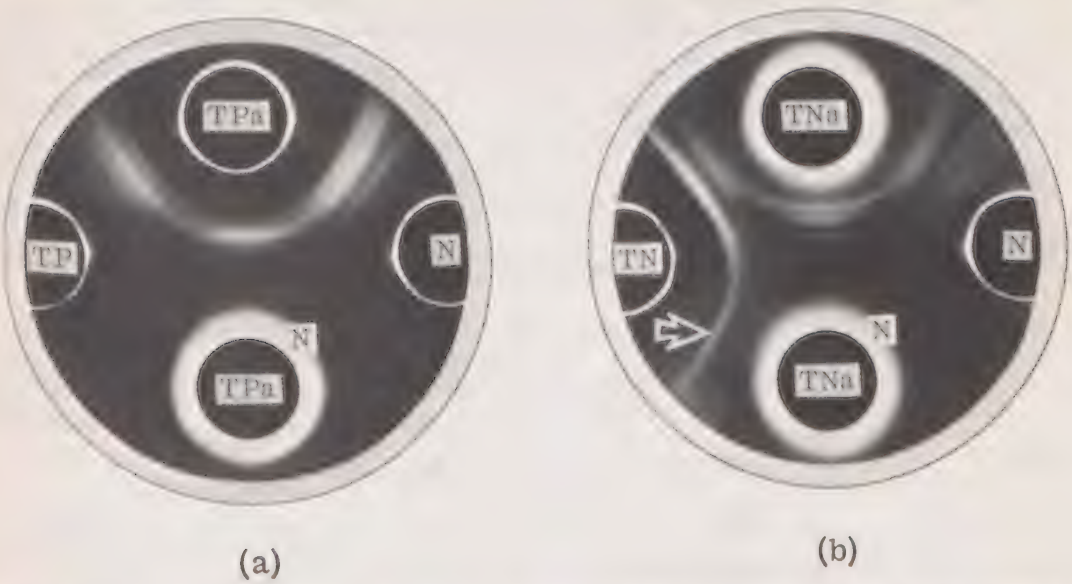

FIG. 2. Agar gel diffusion plate, showing the immunological reactions of foot muscle antigens of the Nelspruit population to antiserum of (*a*) *B. tropicus* and (*b*) *B. truncatus*. Note the " non-identity " reaction with the latter. TP = well containing *Bulinus tropicus* antigen; TPa = *B. tropicus* antiserum; TN = *B. truncatus* antigen; TNa = *B. truncatus* antiserum; N = Nelspruit population antigen.

Immunological techniques were the same as described in Burch & Lindsay (1970a). Antigens from each of the 2 *Bulinus* populations were tested by G. K. Lindsay for " identity " and " non-identity " reactions with antisera from diploid *B. tropicus* (n = 18) (DeVilliers cement reservoir, Malelane, Transvaal, S. Africa) and polyploid *B. truncatus* (n = 36) (Iflaka Bilharzia Project area, Behaira Province, Egypt) and *B.* sp. (n = 72) (Lagaruba River, 16 miles north of Addis Ababa on the Debra Marcos Road, Ethiopia).

RESULTS

Both snail populations studied here contained only normal diploid (n = 18) specimens, which moreover, gave " identity " reactions with *Bulinus tropicus* antiserum (Fig. 2) and " non-identity " reactions with the 2 polyploid antisera. Similar results were obtained with the Lake Sibayi snails when they were tested with antigens of *B. tropicus* from South Africa and from Rhodesia, and the tetraploid *B. coulboisi* from Tanzania (Burch & Lindsay, 1970b). Results of the susceptibility studies are given in Table 1. Some descendants of the Nelspruit population of *Bulinus* were susceptible to each of our 3 strains of *Schistosoma haematobium*. Three of 108 specimens of *Bulinus* from Lake Sibayi were found infected with the Iranian strain of parasite, although we found no snails infected with the other 2 strains of *S. haematobium*[6]. The development of the parasite in these positive snails seemed normal since the prepatent period and the number of cercariae emerged were within the range observed in normal snail hosts.

[6]Pitchford (pers. comm.) also obtained an infection with *Schistosoma mattheei* in a *Bulinus* s.s. specimen from Lake Sibayi.

TABLE 1. Susceptibility of diploid South African *Bulinus* exposed to 3 strains of *Schistosoma haematobium*

Snail population	Origin of *S. haematobium* strain	No. of Snails		
		Exposed	Survived	Positive
Nelspruit	Egypt	65	55	5 (9%)
	Iran	40	12	1 (8%)
	Rhodesia	153	73	7 (10%)
L. Sibayi	Egypt	50	41	0
	Iran	140	108	3 (3%)
	Rhodesia	50	33	0

DISCUSSION

The planorbid subgenus *Bulinus* s.s. has a geographical distribution which extends from the Mediterranean and Middle Eastern countries to southern South Africa. However, its species have been known to serve as intermediate hosts for *Schistosoma haematobium* only north of the Sahara. The subgenus generally has been considered to comprise 2 groups of species, the more northerly *B. truncatus* group, which is tetraploid and readily capable of being infected with *S. haematobium*, either naturally or experimentally, and the more southerly *B. tropicus* group, which is diploid and generally believed to be refractory to infection with *S. haematobium* (e.g., see Dawood & Gismann, 1956; Lo, 1968). The 2 species groups are very similar morphologically, often nearly indistinguishable, but in the last several years they have been separated mainly by the shapes of the mesocones of the 1st lateral radular teeth (Mandahl-Barth, 1957, 1960, 1965; Schutte, 1965, 1966) and chromosome numbers (Burch, 1964, 1967; Natarajan, Burch & Gismann, 1965). Recently, it was shown that the radula characters and chromosome numbers of certain bulinine populations do not always show a perfect correlation, and for those species with the *truncatus*-type radular teeth, but diploid chromosome numbers characteristic of the *tropicus* group, a 3rd species group, the *natalensis* group, was proposed (Brown et al., 1967). However, electrophoretic and immunological studies (Burch & Lindsay, 1967, 1970a, b) of foot muscle extracts of various bulinine populations have indicated that *B. natalensis* is a member of the *B. tropicus* group, and it seems to us that there is no justification for including diploid bulinine snails with some *truncatus*-like morphological and parasitological characteristics in either the *truncatus* group (Van Eeden, in Pitchford, 1965) or a separate species group (Brown et al., 1967), although *B. natalensis* perhaps should be regarded as a valid species belonging to the *tropicus* species group.

Our results confirm the previous reports of a South African *Bulinus* s.s. population being susceptible to *Schistosoma haematobium*, and we have shown that another snail

population from South Africa is susceptible to at least the Iranian strain of the parasite. Porter (1938) reported a successful infection of laboratory bred "*B. tropicus*" in South Africa, long looked upon with skepticism. Her snails may well have been similar to our populations, i.e., susceptible diploid species of the *B. tropicus* group.[7] Our observations lead us to speculate that the susceptible polyploid *truncatus* group to the north had a diploid ancestor which might have been very similar to these southern diploid susceptible populations.

ACKNOWLEDGEMENTS

We wish to thank E. G. Berry, J. Massoud and L. Husting for the strains of *Schistosoma* used here, and C. A. Wright, D. S. Brown and G. Oberholzer for the Lake Sibayi *Bulinus* specimens. Thanks are also due G. K. Lindsay for making the immunological tests, and to S. K. Wu for the shell photographs.

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[7]Teesdale (1962) also reported a laboratory infection of *B. tropicus* ("*alluaudi*"), but the tetraploid *truncatus* group species *B. coulboisi* (n = 36) occurs widely in Kenya and is morphologically difficult to distinguish from *B. tropicus*. Teesdale's report for *B.* "*alluaudi*" should be confirmed.

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THE MORPHOLOGY OF *ALCITHOE ARABICA* (GASTROPODA: VOLUTIDAE)

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ABSTRACT

Alcithoe arabica (Gmelin) is the common large volute of the North Island of New Zealand. It lives at and below low tide on a muddy or sandy substratum, and feeds on various Mollusca which it envelops in its large foot. Though the animal and shell are modified for burrowing, they are not greatly specialized.

The mantle cavity is typical of the Neogastropoda, and the hypobranchial gland produces a purple secretion. The gut of *Alcithoe* is similar to that described in other members of the Volutidae. Key features are the short, thick-walled proboscis, powerful buccal mass, much reduced mid-oesophagus, and long convolute gland of Leiblein. The small U-shaped stomach has tall, plate-like structures in the anterior section and a simple intestinal half. An anal gland is present. An account of the morphology and histology of each organ of the alimentary canal is given. The female genital tract is unusual in having a relatively short capsule gland, but in other features agrees with most of the other Neogastropoda that have been described. The albumen gland and ingesting gland are both large, and the latter is divided into 2 distinct regions histologically. The egg capsules are large and solitary and are covered with a calcareous shell. An open prostate gland is the most unusual feature of the male genital system and the ejaculatory and penial ducts show remnants of an originally open groove. The kidney is similar to that of *Oliva* in having 2 distinct glandular areas and the nervous system is not unlike that of certain other volutes.

INTRODUCTION

The large, colourful volutes have long been popular with shell collectors, but the morphology and habits of only a few species are known. The family is largely tropical, though several genera extend into temperate and even Antarctic seas. They usually live in the sublittoral and extend to considerable depths. Volutes typically plough their way through gravel, sand or mud in search of prey and possess modifications suited to this mode of life. The Volutidae are neogastropods and are placed in the superfamily Volutacea by Thiele (1929) along with the Mitridae, Olividae and Cancellaridae which are considered to be the most specialized and highly evolved of the rachiglossate Prosobranchia.

Investigations into the morphology of the Volutidae were first made by Quoy & Gaimard (1833) who gave some anatomical details and their beautiful colour illustrations of the living animals have often been reproduced in later texts. Fischer (1858, 1867, 1879) investigated the animal of some volutes and Bouvier's (1887a) careful studies on the gastropod nervous system included that of *Cymba*. Perrier's (1889) investigations on the gastropod renal organ also included *Cymba*. In 1900, Woodward described the gross morphology of several species of volutes, and since that date several further investigations have been made, the more important of which are listed below. In most investiga-

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tions the complete anatomy of the animal was not examined. Name changes have occurred in some cases, the name used in the publication cited is given in brackets after the name currently in use.

Bouvier (1887a), *Cymba pepo pepo* (Solander) [*Melo neptuni* Gmelin].

Fischer (1858), *Halia priamus* Meuschen.

Fischer (1867), *Lyria deliciosa* (Montrouz).

Fischer (1879), *Voluta musica* Linnaeus.

Poirier (1885), *Halia priamus* Meuschen.

Perrier (1889), *Cymba pepo pepo* (Solander) [*Voluta neptuni*].

Woodward (1900), *Adelomelon ancilla* (Solander) [*Voluta* (*Cymbiola*)], *Neptuneopsis gilchristi* (Sowerby), *Voluticorbis abyssicola* (Adams and Reeve) [*Volutilithes*].

Pace (1902), *Voluta musica* Linnaeus, *Lyria deliciosa* (Montrouz) (comments on Fischer's description), *Neptuneopsis gilchristi* Sowerby, *Voluticorbis abyssicola* (Ad. & Rve.) [*Volutilithes*], *Adelomelon ancilla* (Solander) [*Cymbiola*], *Halia priamus* Meuschen (comments on previous description).

Fleure (1912), *Cymbium melo* (Solander) [*Melo indicus* Gmelin].

Cooke (1922), A review of the radulae of the Volutidae.

Eales (1923), *Harpovoluta charcoti* (Lamy) [*Volutharpa*].

Clench & Turner (1964), *Odontocymbiola americana* (Reeve), *O. magellanica* (Gmelin), *Adelomelon ancilla* (Solander), *A.* (*Weaveria*) *riosi* Clench & Turner, *A.* (*Pachycymbiola*) *brasiliana* (Lamarck), *Voluta ebraea* Linnaeus, *Zidona dufresnei* (Donovan), *Aurinia florida* (Clench & Aguayo), *A. kieneri* Clench.

The bibliographic references to the species listed above are not repeated in the text below.

The following account describes the morphology of the common, large, New Zealand volute, *Alcithoe arabica* (Gmelin, 1791), the type species of the genus *Alcithoe* (H. & A. Adams, 1853). No previous accounts of its anatomy have appeared, though the radula was described and figured by Hutton (1883, p 121) and later by Powell (1928, p 363, fig. 1). Suter (1913) described the shell and head-foot and gave a full list of synonymy. He later (1919) provided a description of the egg capsule and the embryonic shell, together with notes on the mode of feeding of *Alcithoe*. Graham (1941a) has also given a detailed account of the egg capsule and embryo of *A. arabica*.

The distribution, shell variation and ecology of this species are difficult to discuss as there are several closely allied nominal " species " which may prove to be only geographical or ecological varieties of *Alcithoe arabica*. The typical, heavily nodulated form is found in most North Island harbours with the exception of Wellington Harbour, and throughout the east coast of the North Island from north of East Cape to Doubtless Bay. Other forms occur throughout New Zealand. The depth range of typical *arabica* is not great but closely allied forms are found on the continental shelf and *A. larochei* Marwick has been recorded from over 300 fathoms (Dell, 1963).

The shell of typical *Alcithoe arabica* (Fig. 3) varies between approximately 80 mm and 140 mm in height and has 7–10 heavy nodules on the shoulder of the body whorl. It is yellowish to pale orange in colour, and usually has dark brown or black zigzag markings. Normally there are 4 strong columellar plaits with a weaker one above, and the inner lip is spread over the columella below to form a broad plate.

MATERIALS AND METHODS

Specimens used in this study were collected at Westmere Reef, Auckland Harbour and in Porirua Harbour on the Wellington west coast. The mode of life was observed in the field at both of these localities. The animals were dissected alive, and after fixation with Bouin's fluid, formalin and alcohol. Material for sectioning was fixed in Bouin's fluid and double embedded by Peterfi's celloidin-paraffin method (see Pantin, 1962). Sections were cut at 6-10 microns and stained with Mallory's triple stain.

ECOLOGY

In the Auckland and Porirua Harbours *Alcithoe arabica* is usually found at extreme low water during spring tides. The combination of patchy distribution, scarcity and burrowing habit of this animal make it difficult to assess the size of any given littoral populations. In addition, it is apparent that the majority of the population is subtidal.

In the areas studied *Alcithoe* not only lives on the lower parts of extensive mudflats but also on steeper areas near headlands where there is a considerable flow of water and the substratum often has a high gravel and pebble content. Few specimens were taken from stable mudflats where the substratum is of very fine grade and is often compacted and bound together by the roots of *Zostera*.

A related form, *Alcithoe swainsoni* Marwick, often washes ashore on the Wellington west coast beaches in large numbers. Occasional specimens are found living at extreme low water but the vast majority of the population must occur subtidally, probably beyond the breaker zone. In this locality the substratum is composed entirely of fine, clean sand. In the north east of the North Island, typical *A. arabica* replaces *A. swainsoni* in coastal sandy areas.

Alcithoe arabica has now virtually disappeared from many areas in the vicinity of Auckland where it was reported as being abundant a generation ago. This may possibly be due to pollution but the attraction to collectors of its handsome shell may also have been an important factor in its depletion. The existance of corroded and therefore unattractive individuals, still living in the highly polluted upper reaches of the Auckland Harbour supports the latter view.

FEEDING

Alcithoe has been observed feeding on a variety of molluscs which usually range from 2-4 cm in length and width so that the prey can be gripped readily by the large foot (Fig. 3). The actual mode of entry to the prey is uncertain, as there is no indication of drilling as found in the Muricidae and certain other carnivorous families (Owen, 1966), nor is the shell levered open as has been observed in *Busycon* (Magalhaes, 1948) and *Buccinum* (Hancock, 1960).

The opening of bivalve prey is probably achieved by continuous pressure being applied to the valves, and to facilitate this the bivalve is held with its hinge line uppermost. Gastropods are held with the spire buried in the centre of the foot and the aperture facing anteriorly. Access to a gastropod like the turbinid *Lunella* with its tightly fitting, calcareous operculum could hardly be obtained by gripping the operculum with the foot as it is extremely doubtful that sufficient purchase could be obtained. Probably the prey is held until it is partially asphyxiated. *Alcithoe* is a slow-moving animal and such actions as feeding and ovipositing appear to be exceedingly long processes.

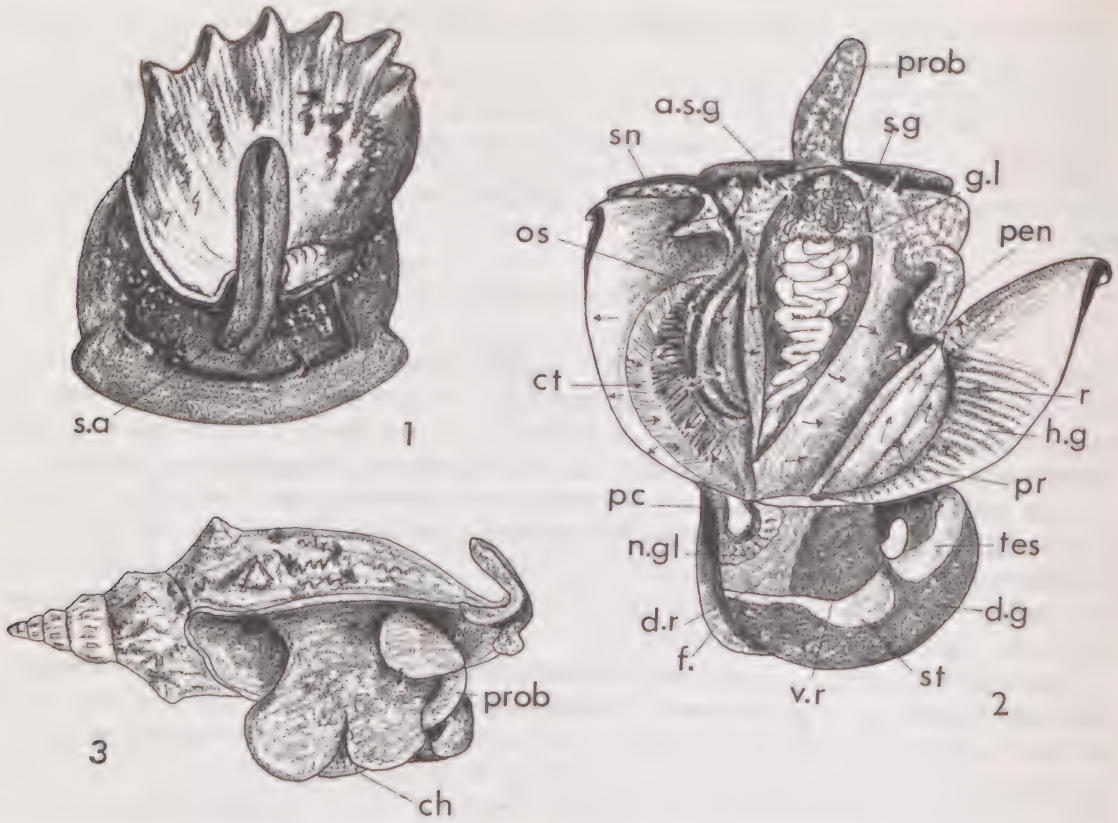


FIG. 1. Anterior view of living *Alcithoe*. FIG. 2. Dorsal view of a male with mantle cavity and cephalic cavity opened. FIG. 3. Lateral view of *Alcithoe* feeding. Arrows indicate ciliary currents.

a.s.g., accessory salivary gland; ch., *Chione stutchburyi;* c.t., ctenidium; d.g., digestive gland; d.r., dorsal glandular area of renal organ; f., foot; g.l., gland of Leiblein; h.g., hypobranchial gland; n.gl., nephridial gland; os., osphradium; pc., pericardium; pen., penis; pr., prostate; prob., proboscis; r., rectum; s.a., siphonal appendage; s.g., salivary gland; sn., siphon; st., stomach; tes., testis; v.r., ventral glandular area of renal organ.

Marcus & Marcus (1959) describe a similar mode of feeding in the olivid, *Olivancillaria* (*Lintricula*) *auriculata* (Lamarck) which holds the bivalve *Donax* in its massive foot.

Alcithoe has been observed feeding on the following species: *Chione stutchburyi* (Gray) (Veneridae); *Macomona liliana* (Iredale) (Tellinidae); *Lunella smaragda* (Gmelin) (Turbinidae); *Cominella adspersa* (Bruguiére) (Buccinidae).

In the areas studied *Chione* was the most abundant of the potential food species and it formed the bulk of the diet of *Alcithoe*. It seems likely that *Alcithoe* will feed on any bivalve or gastropod, that is of suitable size and shape, which it encounters buried or on the surface.

EXTERNAL FEATURES

Alcithoe is usually entirely or partially buried in the substratum though it sometimes emerges on to the surface where it slowly creeps about. The broad foot digs into the substratum with a rather slow action which is often broken by long pauses when the animal is uncovered by the tide.

The foot is short, broad and rounded behind. Its front is slightly curved and has small lateral expansions (Fig. 1). A slit along the front edge marks the opening of the anterior pedal gland. The mobile edges of the foot are thin and sensitive to touch. They are brought together when the animal retracts into its shell and serve to close the aperture as there is no operculum. An adequately cryptic coloration is present on the dorsal surface of the head, siphon and mantle lobes and takes the form of a mass of small purple and yellow blotches produced by an alcohol-soluble pigment stored in the epithelial cells. Though the sole of the foot is mostly white there are occasional yellow and purple spots. In the female there is a large circular glandular depression in the sole a little behind the anterior edge of the foot which secretes the calcareous covering of the egg capsules. The long pallial opening on the right is effectively closed by the fleshy lobe of the mantle margin pressing against the dorsal surface of the foot. The mantle margin does not extend past the lips of the shell aperture.

Depth of burrowing is limited by the length of the siphon (Figs. 1, 2, sn.) which never exceeds more than about 4 cm, and always maintains contact with the surface of the substratum. The animal burrows by first thrusting the front of the foot into the substratum and then lifting the shell and head clear so that the foot can be forced further downwards. When the anterior end of the shell is buried the animal burrows obliquely downwards with the outer lip of the shell acting as a plough. The animal may eventually become completely buried with only the tip of the siphon visible, although usually the dorsal part of the shell is exposed. An *Alcithoe* burrowing in sand between tides leaves a broad, short trail which is covered with a copious grey mucus produced by the pedal glands. This mucus helps to bind the substratum and lubricate the passage of the foot. Movement is generally slow, individuals moving a maximum of a few inches between tides, and even when covered with water they only move along slowly.

The flap-like, broad head has short, non-retractile tentacles about 4 mm long, and often projects over the front edge of the foot (Fig. 1). A broad, middle region forms a canopy between the tentacles and represents the enlargement and concrescence of the tentacle bases (Bouvier, 1887). The minute eyes lie on the outside of the tentacles on very short papillae and behind these are wing-like expansions which are also of tentacular origin as they are supplied, like the middle head lobe, by the tentacular nerve. The middle region of the head lobe presumably prevents foreign particles from entering the rhynchostome during burrowing.

A pair of appendages of equal size form a downward extension at the base of the siphon (Fig. 1, s.a.) and tend to close off the opening to the mantle cavity below the siphonal notch. The appendages are usually held together and are bent to the right over the head lobe unless the animal raises itself up on its foot, or if the anterior part of the foot is bent sharply downwards, then the siphonal appendages clasp the lower margin of the shell aperture. No inhalant current could be detected entering the siphon-like structure formed by the appendages.

Tall columnar cells with interspaced mucous cells make up the epithelium covering the head-foot. On the sole of the foot cilia beat posteriorly and a copious mucous supply is produced by the epithelial and rounded subepithelial cells, the latter having fine ducts which transport their secretion to the surface of the sole. An additional supply of mucus is provided by the anterior pedal gland. The secretion from this gland is liberated through a shallow groove mostly lined with typical pedal epithelium and the gland itself is a mass of epithelial and subepithelial mucous cells.

The rest of the integument is non-ciliated except for the siphon which has weak cilia

that do not appear to be important in cleansing. Gland cells on the dorsal surfaces are moderately abundant, though less common on the tentacles. The ventral surface of the head-lobes resembles that of the sole in having a tall, heavily glandular epithelium. The inner surface of the siphon and its appendages have shorter epithelial cells (20 μ high) than those on their outer surface (80 μ high) though they are strongly ciliated and gland cells are not particularly abundant.

In transverse sections of the highly muscular siphon no clearly defined zones of muscle are apparent, most of the muscle being a mixture of variously orientated fibres. The siphonal appendages are composed of connective tissue and muscles of mixed orientation, but the head fold and tentacles are mostly connective tissue.

Though the dorsal surface of the head lobe and foot are not ciliated, mucous-bound sediment is prevented from accumulating by the movements of the head beneath the siphonal appendages, and by the head-lobe moving over the anterior part of the foot. A rejection current passes from left to right across the right mantle edge and the base of the head, and then posteriorly to the exhalant aperture. The inner surface of the siphon and its appendages are cleansed by cilia beating toward their outer edges. Cilia on the mantle over the columella remove particles to its outer edges from where they are brushed off by the substrate as the animal moves.

THE MANTLE CAVITY

The broadly triangular mantle cavity (Fig. 2) is like that of other neogastropods in plan, but upon this basic design are imposed the specialised requirements of a burrowing prosobranch. Efficient cleaning, together with the structural and behavioural closing mechanisms, prevent sediment clogging the delicate respiratory and sensory organs. In addition, the liberal production of mucus over the entire pallial epithelium binds any stray sediment which can then be carried to the exhalant opening of the mantle cavity.

While burrowing, part of the mantle cavity is closed by the siphonal appendages, as mentioned above, and the rest of the elongate opening is closed by the broad, muscular lips of the mantle edge. These press against the dorsal surface of the foot so that the pallial cavity is effectively sealed in life, apart from the siphonal aperture and the small exhalant opening behind.

The disposition of the pallial organs is similar to that of other Neogastropoda (Fig. 2). A bipectinate osphradium (os.) and a monopectinate ctenidium (ct.) lie on the left, a broad, pleated hypobranchial gland (h.g.) on the roof and, on the right, the rectum (r.), anal gland and genital duct (pr.). The renal organ bulges into the posterior part of the mantle cavity where it opens by way of a median slit. The siphon becomes confluent with the mantle cavity at the base of the osphradium and a ridge of tissue on the right directs the entering water current to the left over this organ and the ctenidium.

The Osphradium and Ctenidium. The osphradium is rather narrow in comparison with that of many other neogastropods and it is about 2/3 the length of the ctenidum. There are about 200 brown leaflets on either side of the poorly pigmented axis and each receives a branch of the osphradial nerve. Cilia on the leaflets (Fig. 4) on both sides, beat away from the axis on both the free edge, which hangs into the mantle cavity, and the lateral surfaces. Each leaflet is constructed in a similar fashion to that of *Neptunea antiqua* (Linnaeus) (Yonge, 1947).

The outer edge (o.a.) is horizontally ridged, and this, together with a narrow band just above the fixed edge, is transparent and ciliated. The main sensory area (i.a.) forms

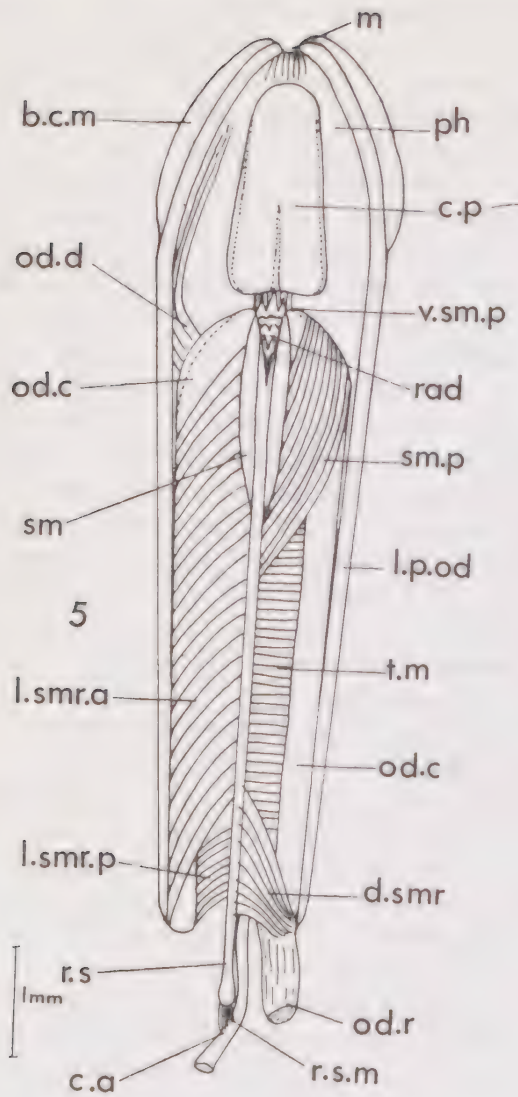
the bulk of the leaflet, is brown and is rather weakly ciliated on the lateral faces, though there is a tract of powerful cilia along the free edge. A narrow, deeply pigmented groove separates the outer and inner areas. The epithelium of the outer and attached areas is similar to that of the corresponding surface in *Neptunea* except that there is no clear division into ciliated and glandular portions. *Alcithoe* has powerful cilia over the whole of the glandular area which is provided with liberal quantities of both mucous cells and gland cells containing red staining granules. The epithelium of the sensory area is very complex and difficult to interpret owing to the large number of nuclei and different cell types present. Occasional swollen mucous cells and narrower red-staining gland cells, both with basal nuclei, occur on the lateral faces, though they are more abundant on the free edges. The majority of the epithelial cells are non-ciliated, pigmented, supporting cells with central nuclei. Ciliated cells are scattered over the lateral surfaces and are abundant on the free edge. Sensory cells are presumably scattered throughout but these could not be differentiated with certainty. A central blood space between the 2 epithelial layers contains numerous amoebocytes and a thin layer of dense connective tissue fibres keeps the filaments rigid. The epithelium covering the central axis is continuous with that of the free edge of the filaments, although it is weakly pigmented and poorly ciliated.

There is nothing unusual in the structure of the yellowish-white ctenidium with its broadly triangular filaments. The ciliary currents of the filaments are like those of *Buccinum* (Yonge, 1947, p 498). Small mucus-secreting goblet cells are abundant in the abfrontal ciliated zone and common on the lateral ciliated fields, but are scarce over the rest of the surface of each filament. The general structure of the filaments is very similar to that described by Dakin (1912) in *B. undatum*.

The ciliation of the remainder of the mantle cavity (Fig. 2) is like the majority of monopectinate prosobranchs (Yonge, 1947). Cilia on the hypobranchial gland and floor of the mantle cavity carry waste particles to the right side where they are removed from the pallial cavity through the exhalant opening.

The Hypobranchial Gland. This gland (h.g.) lies on the roof of the pallial cavity and can be divided into 3 sections, 2 posterior ridged areas and an anterior smooth portion. The middle portion of the gland is the most conspicuous and lies opposite the anal gland and the anterior half of the pallial gonoduct. Three types of cells (Fig. 8) can be distinguished in life in this area, the majority being yellow-brown to grey and transparent. Studded amongst the transparent cells are abundant white cells which give this area a general white appearance. The white cells exist in 2 phases (translucent and dense), but there is no clear-cut distinction between them. Small narrow, dark red-brown cells are also scattered throughout the gland. The transparent cells are of 2 types, one stains weakly in Mallory's triple stain, showing fine pink granules (t.c.) while the other is of the goblet cell type (g.c.) and secretes a non-staining mucus. The white cells (w.c.) stain according to their phase of secretory activity, either purple, purplish-red, or orange. The purple staining stage probably corresponds to the young semitransparent white cells. In these the secretory material has not broken up into granules but it begins to do this in the purplish-red cells while the orange staining phase is filled with large granules. These cells and the mucus-secreting cells have basal nuclei but the 3rd type (r.c.) have central nuclei, are very narrow and contain a mass of fine greenish-straining granules. Small, ciliated, supporting cells appear between the glandular cells and these have very narrow cell bodies which expand at their distal ends where their nuclei are situated.

The posterior ridged portion of the gland and the anterior smooth area do not have the white cells of the middle area. The anterior smooth portion begins a little inside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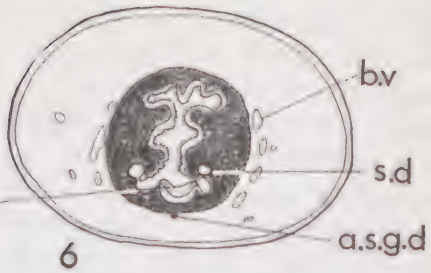
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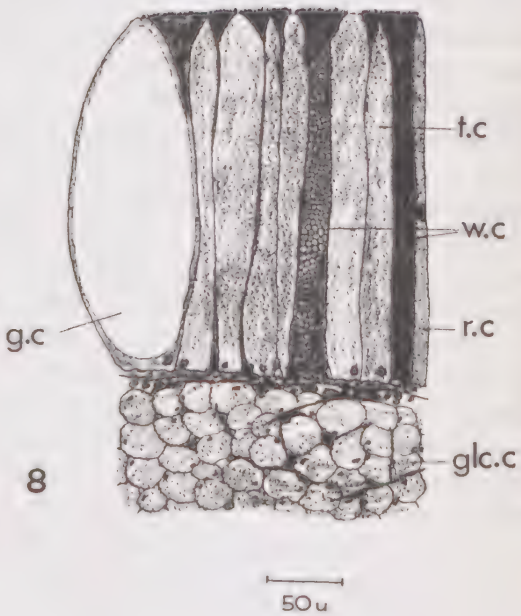
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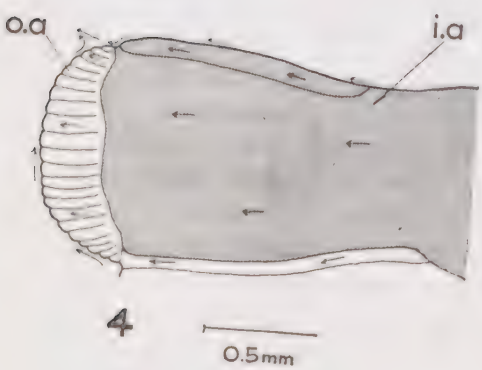
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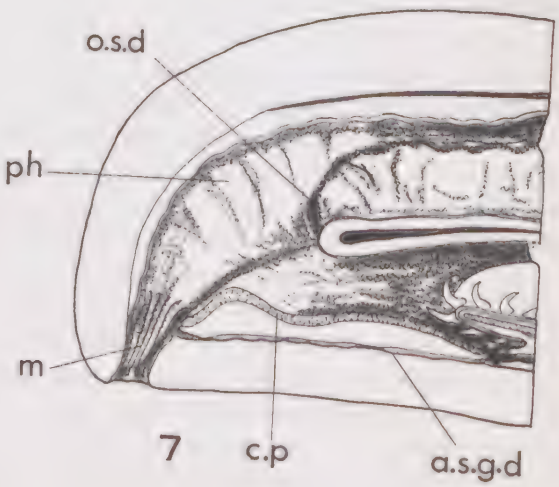
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the mantle edge and also borders the gill and the white central area. It contains shorter cells than those of the rest of the gland and these are all clear in life apart from the occasional narrow red-brown cells. Sections reveal 2 types of transparent cells in this anterior area which correspond with those of the middle area but swollen vacuolate cells make up the majority of the epithelium. The posterior area also resembles the middle portion in the types of transparent cells present, but a 3rd type also exists which contains bright-red granules.

The copious secretion liberated from the hypobranchial gland has a pungent musty odour. The white cells liberate a thick, dense-white mucus which changes rapidly to yellow, then slowly to green, and then through red to a deep purple after 3–4 hours. This change progresses only as far as green in the dark. The secretion from the other cells is a thick mucus which has a brownish-yellow tinge.

Between the glandular cells and the outer cuboidal epithelium of the pallial roof is a layer of connective tissue which contains a few muscle fibres, a mass of glycogen cells (Ronkin, 1952) (glc.c.) and blood vessels. A thin layer of longitudinal muscle, with occasional transverse fibres, lies below the outer epithelium and presumably serves to retract the mantle margin.

THE ALIMENTARY CANAL

The Proboscis and Buccal Mass

The Proboscis. The mode of feeding by grasping the prey between the lobes of the foot necessitates only a short proboscis (Fig. 3). The rhynchostome is overhung by the canopy-like middle lobe of the head. The passage of the proboscis through this opening is lubricated by a pad of very large mucous cells on the ventral lip while the whole of the opening, as well as the ventral surface of the head lobe, is also richly glandular. The fully extended proboscis (Fig. 2, prob.) is only about 2.5 cm long and the reddish musculature of the odontophore and pharynx can be seen through the distal wall of the fully extended organ. Although the surface of the proboscis is pigmented in a similar fashion to that of the foot, the epithelium is much shorter (40–60 μ dorsally and 25–40 μ ventrally). It is lined by cuticle ventrally and the dorsal and lateral surfaces have short cilia. There are numerous gland cells, 3 types being present. Mucous cells with broad colourless vacuoles are interspaced amongst gland cells with red or orange granules and occasional narrow cells with paler blue, granular contents. The supporting cells are relatively much wider than those of the foot and have large nuclei variably situated from their bases to about mid-way along the cell. Blue staining, subepithelial gland cells also occur

FIG. 4. Lateral view of osphradial leaflet. FIG. 5. Schematic diagram of the odontophoral muscles and floor of the buccal cavity. FIG. 6. Transverse section of the proboscis through the buccal cavity. FIG. 7. Longitudinal section of the anterior end of the proboscis. FIG. 8. Cells of the middle region of the hypobranchial gland. Arrows indicate ciliary currents.

a.s.g.d., accessory salivary gland duct; b.c.m., buccal circular muscle; b.v., blood vessel; c.a., proboscidial artery; c.p., chitinous plate; d.smr., dorsal subradular membrane retractor muscle; g.c., goblet cell; glc.c., glycogen cell; i.a., inner sensory area of osphradial leaflet; l.p.od., lateral protractor muscle of odontophore; l.smr.a., anterior portion of lateral subradular membrane retractor muscle; l.smr.p., posterior portion of lateral subradular membrane retractor muscle; m., mouth; o.a., outer ciliated area of osphradial leaflet; od.c., odontophoral cartilage; od.d., cartilage divaricator muscle; odont., odontophore; od.r., odontophoral retractor muscle; oes., oesophagus; o.s.d., opening of salivary ducts; ph., buccal cavity; rad., radula; r.c., red-brown cell; r.s., radular sac; r.s.m., radular sac muscle; s.d., salivary duct; sm., subradular membrane; sm.p., subradular membrane protractor muscle; t.c., transparent cell; t.m., transverse muscle; v.sm.p., ventral subradular membrane protractor; w.c., white cell.

abundantly below the epithelium, especially dorsally and laterally. The mucous cells are particularly common ventrally in the middle part of the proboscis, but in the posterior portion and in the sheath they are very abundant at the expense of the other gland cells. In the anterior part of the proboscis the epithelium is composed mainly of non-glandular columnar cells.

The majority of the retractor muscles of the proboscis are attached to the muscular wall of the proboscis sac, and although this forms part of the everted proboscis, the walls are much thinner (only 0.2 to 0.5 mm compared with 2.0 to 2.5 mm in the outer portion). This change in thickness takes place abruptly and corresponds with the posterior limit of the muscle fibres which bind the oesophagus and pharynx to the proboscis wall in the anterior portion. The muscles in the proboscis wall are largely longitudinal in orientation, although scattered bundles of oblique and transverse fibres also occur.

A single, large, retractor muscle on the floor of the cephalic sinus is fixed to the ventral proboscis wall slightly to the left. Two massive lateral retractor muscles are attached to the left and right sides of the roof of the cephalic sinus and some small lateral and latero-dorsal retractor muscles are also present. In addition, a number of ventro-lateral retractor muscles combine with the odontophoral retractors before the latter become anchored to the body wall.

The Mouth and Buccal Mass. The mouth (Figs. 5, 7, m.) is situated ventrally at the tip of the proboscis. While the odontophore is retracted, it remains small but its interior is thrown into numerous pleats which allow the mouth to open widely and accommodate the odontophore during feeding. Behind the mouth is the small, muscular buccal cavity (Fig. 7, ph.) and its floor is a cuticle-lined plate (c.p.) with raised lateral edges which terminates just behind the mouth. Beneath the anterior edge of this plate is the minute opening of the accessory salivary gland duct (a.s.g.d.), while overhanging it is the oesophagus (oes.) with its associated glandular dorsal folds. The salivary ducts (s.d.) discharge laterally just in front of the oesophageal opening (a.s.d.). There is no dorsal sclerite as seen in the Muricidae (Carriker, 1943; Wu, 1965), no papilla and no vestibule or distinct peristomal rim to the mouth as described in *Urosalpinx* (Carriker, 1943).

The muscles of the anterior part of the proboscis have been described in some rachiglossans, namely *Sycotypus canaliculatus*(Linnaeus)(Herrick, 1906), *Urosalpinx cinerea* Say (Carriker, 1943), and *Buccinum undatum* Linnaeus (Dakin, 1912; Wilsmann, 1942).

The arrangement of odontophoral muscles in *Alcithoe* shows a general resemblance to that of the other described rachiglossans. Although most similar to *Urosalpinx*, there are differences due to the relatively longer odontophore and shorter radular sac. The same terminology employed by Carriker will be used here, and since Carriker gives a full description of the functions of the various muscles, this aspect will not be pursued at length.

The dorsal buccal cavity and the odontophore are roofed by a layer of transverse muscles attached to the proboscis wall by thin buccal tensor strips (Fig. 10, b.t.m.). These muscles are readily separated from the rest of the buccal muscles by their white colour, most of the others being pink owing to the presence of myoglobin (Read, 1966). The transverse muscles encasing the odontophore dorsally are attached ventrally to the oesophagus but the odontophore is free to move within this sheath.

The pink, longitudinal muscles making up the wall of the buccal cavity are supplemented anteriorly by a ring of circular muscles, the buccal circular muscle (Fig. 5, b.c.m.). The pink muscles of the buccal wall are attached to the dorsal transverse muscle sheet by white

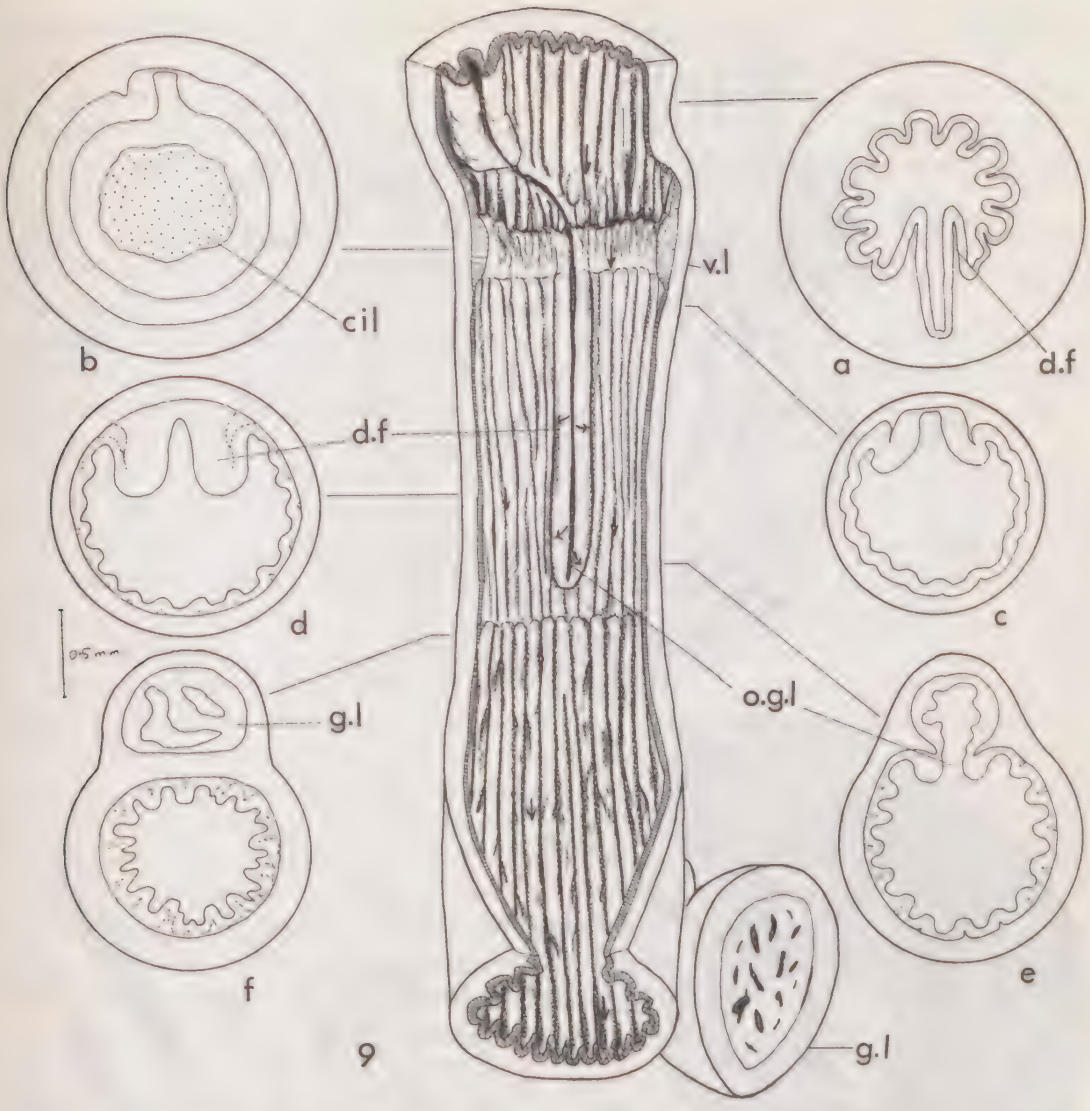
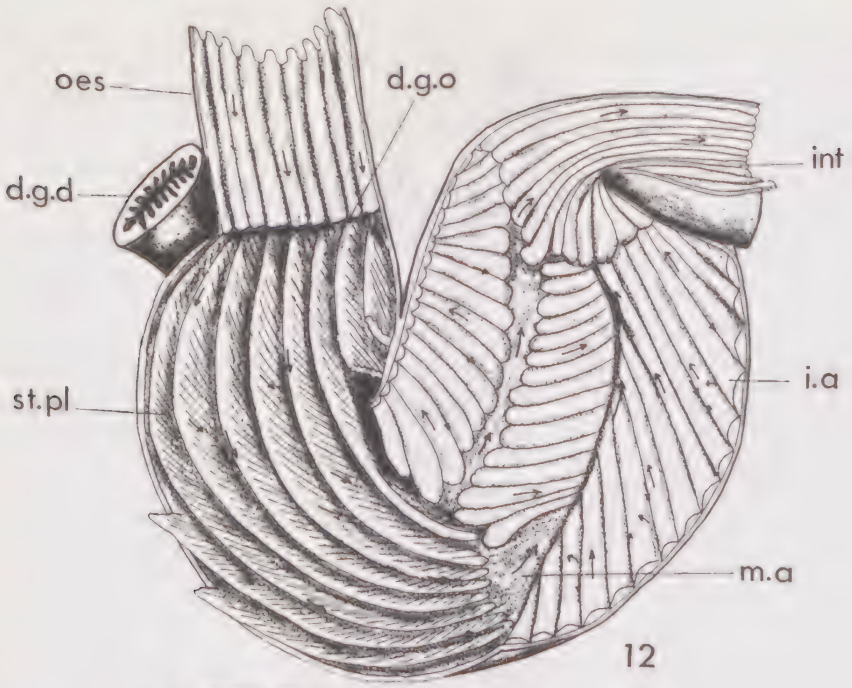


FIG. 9. Middle oesophagus opened ventrally with transverse sections a to f at the levels indicated. Arrows indicate ciliary currents.

cil., cilia; d.f., dorsal folds; g.l., gland of Leiblein; o.g.l., opening of gland of Leiblein; v.l., valve of Leiblein.

muscle fibres and continue behind to form the lateral (l.p.o.d.) and ventral odontophoral protractor muscles (Fig. 10; v.p.o.d.), which lie outside the other odontophoral muscles. On the floor of the buccal cavity is the chitinous plate (c.p.) referred to above, and running parallel to its edges are the cartilage divaricator muscles (od.d.), which are seen as a pair of low ridges. While feeding, the odontophore, which is about 10 mm in length, slides back and forth over the chitinous plate. It is pulled forward by the powerful, sheet-like, pink protractor muscles fixed on to the large, curved ends of the odontophoral cartilages (od.c.). A thin sheet of transverse muscle covering the dorsal surface of the odontophore lies between the 2 lateral odontophoral protractor muscles and this, together with the protractors, is connected to the odontophoral cartilages mid-laterally.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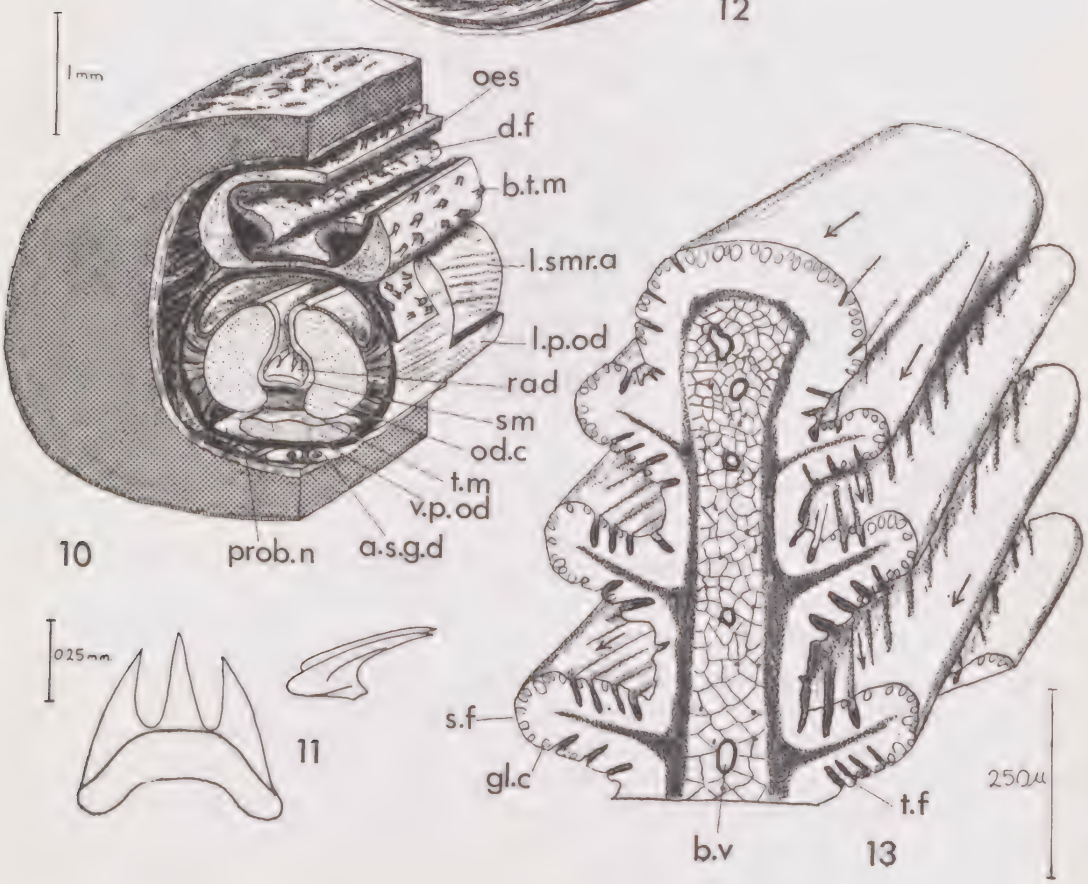
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Backward movement of the odontophore is achieved by contraction of the odontophoral retractors (od.r.), a pair of massive, white muscles which are composed of 2 elements. The dorsal portion of each of these muscles is attached superficially to the proboscis sheath and they finally become embedded close together in the floor of the cephalic cavity. The ventral portions are more strap-like and each is embedded in the floor of the proboscis sheath.

Forward movement of the radula is effected by a pair of triangular, dorsal subradular membrane protractor muscles (sm.p.) which lie dorsally with their posteriorly pointing apices marking the point of closure of the radular sac (r.s.). The fibres of these muscles intermingle below the subradular membrane and the radular sac, to which they are attached, with those of the lateral subradular membrane retractor muscles (l.smr.a., l.smr.p.). The protractors are attached to the anterior portion of the cartilages on their dorso-lateral surfaces. These muscles are not present in *Urosalpinx*, but are found in *Buccinum*.

The lateral subradular membrane retractor muscles are the largest muscles of the buccal mass, for it is these that provide the force for the rasping action of the radula. They are divided into anterior and posterior sections, the former (l.smr.a.) being attached to the outer lateral and latero-dorsal surfaces of the odontophoral cartilages along all but their most anterior portion, and to the subradular membrane and radular sac. The posterior section (l.smr.p.) of this muscle is fixed to only the posterior 1/3 of the radular sac and is attached to the ventral surface of the last portion of the odontophoral cartilage where it replaces the transverse muscle (t.m.). The dorsal subradular membrane retractor muscle (d.smr.) is bulky and short. It is attached to the base of the radular sac (r.s.) and to the ends of the odontophoral cartilages along with the main odontophoral subradular retractor muscles. In *Urosalpinx* this dorsal muscle is the largest muscle of the odontophore. The ventral subradular membrane retractor muscles (Fig. 10, v.smr.) are attached to the distal end of the subradular membrane below the odontophore and extend back to the posterior ends of the cartilages to which they are fixed. A strip of muscle (v.sm.p.) attached to the proximal end of the subradular membrane curves anteriorly beneath the buccal cavity epithelium when the odontophore is fully retracted, but when it is protracted this muscle presumably acts as a radular protractor, as do the ventral subradular membrane retractor muscles, drawing the subradular membrane over the ends of the cartilages.

The odontophoral cartilages (od.c.) are crescentic in section, about 1 mm deep anteriorly where they come close together, but posteriorly they are only about half this height. The cartilage divaricator muscles (od.d.) are attached to the anterior ends of the cartilages and run forwards as a pair of lateral ridges in the buccal cavity. There is a transverse muscle (Fig. 5, t.m.) between the 2 cartilages which binds them together. A short radular

FIG. 10. Diagrammatic view of the structure of the proboscis just behind the anterior end of the odontophore. FIG. 11. Posterior and lateral views of radular tooth. FIG. 12. The stomach opened dorsally. FIG. 13. Diagrammatic structure of the distal portion of a gastric leaf. The arrows indicate ciliary currents.

a.s.g.d., accessory salivary gland duct; bt.m., buccal tensor muscle; b.v., blood vessel; d.f., dorsal fold; d.g.d., duct of digestive gland; d.g.o., digestive gland aperture; gl.c., gland cell; i.a., intestinal area; int., intestine; l.p.od., lateral protractor muscle of odontophore; l.smr.a., anterior portion of lateral subradular membrane retractor muscle; ma., glandular area of stomach; od.c., odontophoral cartilage; oes., oesophagus; prob.n., proboscis nerve; rad., radula; s.f., secondary fold; sm., subradular membrane; st.pl., gastric leaf; t.f., tertiary fold; t.m., transverse muscle; v.p.od., ventral protractor muscle of odontophore; v.sm.r., ventral subradular membrane retractor.

sac muscle (r.s.m.) is attached to the distal bulb of the sac, which protrudes ventrally behind about 2 mm, and this muscle is fixed to the proboscis artery (c.a.) as in *Urosalpinx*.

The radular sac (r.s.) reaches a length of about 16 mm. Only the central teeth of the radula (Fig. 11) are present, these being tricuspid, with heavy, arched bases. The central cusp of each tooth is slightly longer and narrower than the lateral cusps. The base of each tooth is not only arched upwards, but also forwards so that the bases of the lateral cusps bend backwards while the heavily thickened base of the central cusp is arched forwards. The cusps are almost straight, although a slight forward curve is apparent. At its anterior end, the radula curves over the end of the odontophore and the basal ribbon is reabsorbed in a ventral pocket. The teeth thus separated are disposed of.

The Oesophagus and Salivary Glands

The terminology of the prosobranch oesophagus adopted by Graham (1939, 1941) is used in the following description.

The Anterior Oesophagus. After emerging from the proboscis the short anterior oesophagus bends downwards and, a little in front of the nerve ring, the ducts from the salivary glands enter its lateral walls. Immediately in front of the ring a slight swelling indicates the position of the valve of Leiblein and thus the beginning of the mid-oesophagus.

The most conspicuous feature of the anterior oesophagus is the pair of lateral ridges (Fig. 9a, d.f.) protruding into the lumen in which the salivary ducts are buried. These are covered with a ciliated columnar epithelium containing mucous cells. The dorsal epithelium is shorter with fewer gland cells and is thrown into several low ridges, while ventrally just above the odontophore there are small (8–10 μ high), non-ciliated cuboidal cells. Behind the posterior end of the odontophore the dorsal folds migrate ventrally and the epithelium between them becomes taller (15–25 μ) and weakly ciliated. At about this same level, purplish-red staining cells occur occasionally in the epithelium of the dorsal folds and these become rather more common posteriorly, although they are never very abundant. The ciliated cells are similar throughout the oesophagus and stomach. They are narrow, slightly broader distally and have long central nuclei. Their distal halves are filled with fine, brownish granules and usually there is a purplish zone on their distal edges. The epithelial cells become progressively longer through the anterior oesophagus, reaching about 60 μ on the apices of the ridges just in front of the valve of Leiblein, whereas they are only 35 μ in height above the odontophore. Between the ridges mucous cells are more abundant and the ciliated cells are relatively shorter and wider, and have less conspicuous cytoplasmic granules. The ciliated cells of the dorsal folds are identical in structure, but are taller, being about 60 μ in the anterior part of the proboscis and 80 μ just in front of the valve of Leiblein. A thick coat of muscle surrounds the whole of the anterior oesophagus. This is about 100 μ thick in the proboscis and about 260 μ thick just in front of the valve of Leiblein. The slightly wider inner layer is composed mainly of longitudinal muscle but also contains some circular fibres, while the outer layer is primarily circular muscle. The groove between the dorsal folds in the posterior part of the anterior oesophagus cuts deeply into the muscle coat which is only about 110 μ thick immediately below it (Fig. 9a).

The Salivary Glands. There are 2 types of salivary glands in *Alcithoe* as in the rest of the Volutidae and in the Muricidae. The normal salivary glands (Fig. 2, s.g.), which are homologous with those of the rest of the Prosobranchia, are white clusters of narrow tubules. Each tubule (Fig. 15) is about 50 μ wide with a lumen about 5–15 μ in diameter, and it is surrounded by a very thin sheath of connective tissue. Occasional small, wedge-

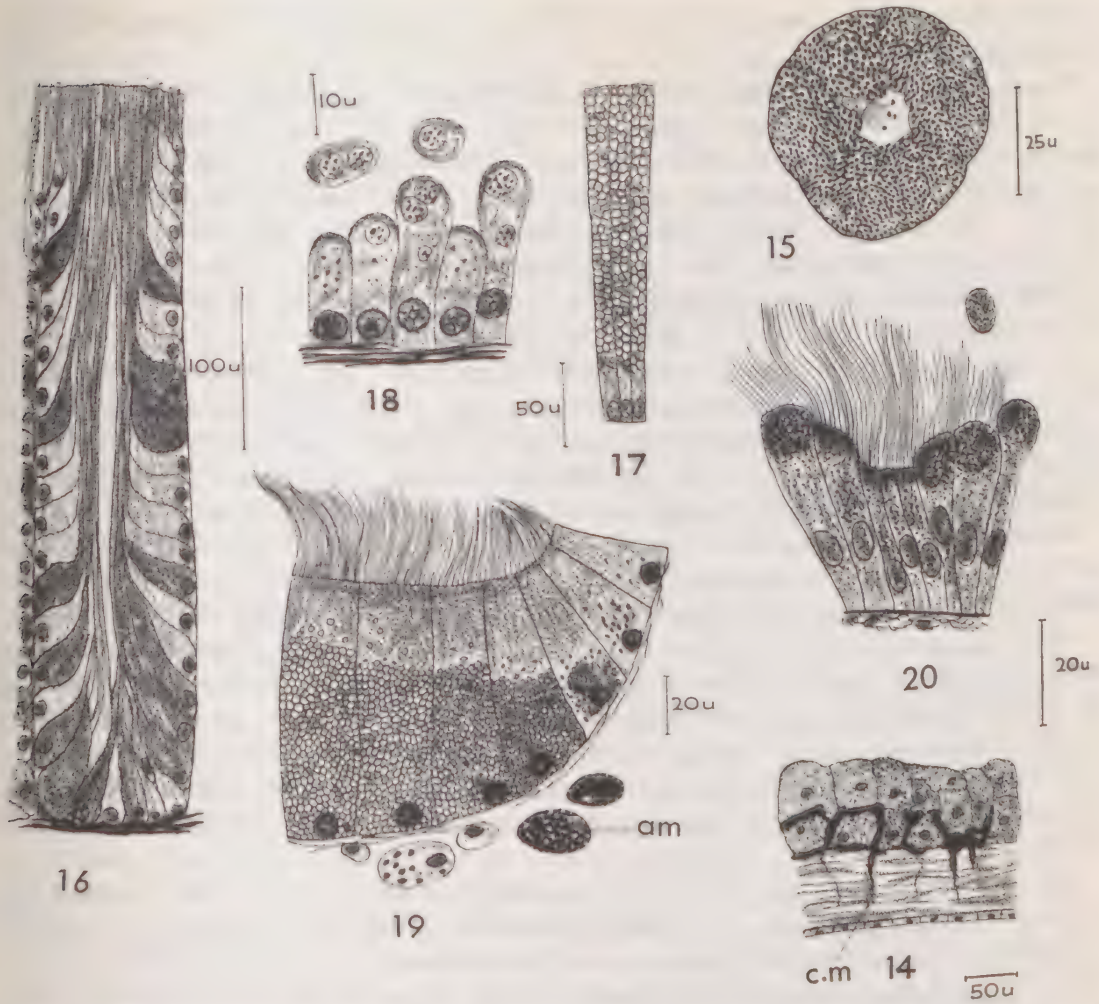


FIG. 14. A portion of the wall of the accessory salivary gland. FIG. 15. Transverse section of a tubule of the salivary gland. FIGS. 16–18. Cells of the gland of Leiblein, (16) anterior region, (17) middle region, (18) posterior region. FIG. 19. Cells of the digestive gland at the distal end of a tubule. FIG. 20. Cells of the anal gland.

am., amoebocytes; c.m., circular muscle.

shaped, ciliated cells occur in the tubules between the gland cells which contain orange-red granules and have basal nuclei. The salivary secretion is collected into bundles of narrow ducts between 25 and 40 μ wide. The ducts within each bundle are encased in a continuous sheath of muscle. They are lined with a low ciliated cuboidal epithelium and drain into the main salivary ducts which are short and run to the oesophageal wall. These are between 140 and 160 μ in diameter, are lined with a ciliated pavement epithelium only 5μ high, and they are surrounded by a thick coat of connective tissue and muscle.

The accessory salivary glands (Fig. 2, a.s.g.) are composed of a pair of convoluted tubules between 0.8 and 1.0 mm in diameter in their outer portions. The wide lumen of each gland is lined with a very flat, non-ciliated pavement epithelium (Fig. 14) only 8 μ high and is surrounded by a layer of circular muscle (c.m.) about 60–80 μ thick. Outside the muscle layer is a layer of glandular tissue interspaced with muscle fibres which is between 80 and 150 μ thick. Each gland cell contains bluish granules and is more

or less spherical with a long very fine duct that enters the cavity of the gland through the lining epithelium.

The accessory salivary gland tubules come into close proximity near the end of the buccal mass, but retain a thin layer of glandular tissue until after they join just behind the cuticulate plate on the floor on the pharynx. The tubule (Fig. 7, a.s.g.d.) then becomes very narrow and opens beneath the anterior edge of this plate. The structure of this gland is very much like that of *Oliva peruviana* Lamarck (Küttler, 1913), but it differs from that of *Nucella lapillus* (figured by Fretter & Graham, 1962, p 159, fig. 97 E) in not having a glandular columnar epithelium lining the tubule. However, these structures in the Muricidae, Olividae and the Volutidae are clearly homologous.

The Mid-oesophagus. The valve of Leiblein (Fig. 9, v. l.) and the constricted portion of the oesophagus that passes through the nerve ring, together with the gland of Leiblein (g.l.) make up the mid-oesophageal region of the gut (Fig. 9). The length of this portion, excluding the discrete gland, is only 7 mm, but the long, glistening-white, coiled gland of Leiblein is one of the most conspicuous parts of the alimentary canal.

Although the valve of Leiblein is much less conspicuous than that of *Nucella* (Graham, 1941), it is very similar in structure. The ciliated ridges of the anterior oesophagus overhang a glandular ring (Fig. 9b) and the long cilia (cil.) issuing from their edges form a cone-like mass in the lumen of the valve. The histology of the glandular area of the valve of Leiblein is similar to that of *Nucella* and other described rachiglossans, although the ventral channel is much more widely open than in most. A narrow, anterior zone of tall mucous cells gives way to a wider posterior zone of taller glandular cells (170-230 μ in height) with deeply staining granules and relatively larger basal nuclei. In both areas the gland cells are supported by narrow ciliated cells with long central nuclei.

The ventrally located dorsal folds of the posterior end of the anterior oesophagus terminate just before the glandular area of the valve of Leiblein. However, the groove between the dorsal folds (the ventral groove) bends sharply to the right, cutting through the ciliated ridges and passes mid-dorsally through the glandular area (Fig. 9b), where it is bordered by low swellings of the glandular epithelium. Similar low swellings (the dorsal folds) accompany the groove through the remainder of the mid-oesophagus (Figs. 9c, d) to the opening of the gland of Leiblein (Fig. 9e, o.g.l.), behind which they coalesce and terminate (Fig. 9f). The outer surfaces of the dorsal folds are ciliated and the epithelium, although much taller (up to 70 μ), is similar to that of the ventral and lateral parts of the mid-oesophagus. These cells are of similar structure to those of the anterior oesophagus, but mucous cells are much more abundant in the epithelium and the purple-red gland cells occur only very occasionally throughout the ciliated surface.

The inner surfaces of the dorsal folds are composed of tall, glandular, non-ciliated cells that are similar to, and continuous with, those of the 1st portion of the gland of Leiblein. On the floor of the ventral groove near the valve of Leiblein there are short cells only 10 μ high, but further back these increase in height and merge with the lateral epithelium (Fig. 9d).

A copious secretion is produced by the epithelium of the mid-oesophagus and, as in the anterior and posterior oesophagus, ciliary currents drive food particles posteriorly. There are, in addition, transversely directed cilia on the dorsal folds which drive particles away from the dorsal groove and thus spill the secretion from the gland of Leiblein into the lumen of the oesophagus. A similar pattern of ciliation is found in most other prosobranchs (Graham, 1932, 1939, 1941).

The muscular coat of the mid-oesophagus is, for the most part, much thinner than that of its anterior counterpart. Around the valve of Leiblein it is about 0.16 mm thick, but along the rest of its length it is only about 0.1 mm thick. The layers of muscles are in reverse to those of the anterior oesophagus, there being a relatively thick, mainly circular layer under a thin sheath of longitudinal muscles. Near the opening of the gland of Leiblein, just behind the nerve ring, the muscle layer thickens slightly, while just behind this opening it binds the gland of Leiblein to the oesophagus.

The Gland of Leiblein. The convoluted, tubular gland of Leiblein is the most conspicuous feature of the cephalic sinus (Fig. 2, g.l.). It arises mid-dorsally and the 1st short portion is bound to the oesophagus. It then passes to the right, bends forward, and then turns back alongside the posterior oesophagus where it is crossed by the posterior aorta. Behind this point the convolutions of the gland become less marked and it ends, rather abruptly, without tapering. This latter portion of the gland is embedded in a spongy connective tissue that fills the posterior half of the cephalic sinus. The total length of the gland is about 50 mm, about 1/3 that of the compact organ, and it is of similar diameter throughout.

The gland can be divided into 3 regions on the basis of its histological structure. The proximal region is about 30 mm long and its cells (Fig. 16) are very elongate and are arranged into multicellular alveoli. Its lumen is subdivided at any one point of 1 or 2 partitions made up of connective tissue and muscle fibres, and the massive development of the glandular epithelium (up to 0.66 mm thick) all but fills the remaining cavities (Fig. 9). Each cell has a bulging base and a very slender neck, and is filled with minute red staining granules when mature. The nuclei of these cells are circular with distinct nucleoli. Immature cells stain bluish and show only a faintly granular cytoplasm. Each multicellular gland is an inpushing of the general epithelium and all of the cell ducts open at the same level. Each alveolus is surrounded by a thin layer of connective tissue fibres. The muscular coat of this region is rather thin (about 50 to 80 μ thick) with inner longitudinal and outer circular fibres.

The secretion from this portion of the gland is white, but rapidly changes to pale brown after being liberated into seawater. A diluted extract of this portion of the gland was tested for its action on a piece of the living gill of the bivalve *Chione stutchburyi* (Gray) and, although there was no immediate effect, a partial breakdown of tissue was observed after 15 minutes and about 50% breakdown had taken place after 12 hours. Control specimens in seawater were still living at the end of this period.

The next portion of the gland is about 10 mm long. The tissue is opaque and yellowish after fixation in formalin, whereas that in the anterior part of the gland is translucent pale orange-red. The cells (Fig. 17) are a little shorter than those of the 1st section (about 110–160 μ high) and are filled with large, red staining granules. These cells are mostly infolded into shallow pits, but they remain more or less similar in size and do not develop long terminal ducts. Subdivision of the lumen occurs as in the proximal region and the muscular coat is also similar.

The entrance to the posterior region is guarded by a muscular constriction formed by a sphincter muscle. The outer muscular coat is much more developed than over the proximal part of the gland, being about 340 μ thick, whereas the overall diameter is slightly less, being about 1.9 mm as compared with 2.0–2.1 mm throughout the rest of the gland. Behind the sphincter the epithelium is composed of irregular, columnar cells only 20–30 μ high, with bluish-purple, finely granular contents (Fig. 18). These cells accumulate greenish granules in their distal ends which are nipped off periodically

and liberated into the lumen of the gland. This epithelium is also largely arranged in multicellular units strengthened by thin layers of connective tissue. A low, ciliated double fold, homologous to the ventral folds in the gland of Leiblein of *Nucella* (Graham, 1941), runs along the ventral side of the posterior portion of the gland and terminates at the sphincter. It is composed of an epithelium like that of the oesophagus, with similar ciliated, mucous and glandular cells. The wide lumen of this portion of the gland is in marked contrast to that of the rest of the gland, but it is also subdivided by transverse partitions.

The Posterior Oesophagus. Just behind the opening of the gland of Leiblein, the low ridges of the mid-oesophagus are replaced by taller, irregular ridges (Fig. 9f) which are not as opaque in life and have a much less abundant supply of mucus. This point marks the beginning of the long posterior oesophagus. Large pieces of food are often found stored and undergoing digestion in this region, the enzymes responsible presumably being derived from the gland of Leiblein. Ciliary currents then carry the broken-down particles to the stomach where digestion is completed. Near the stomach the ridges increase in height and show some secondary folding. The epithelium of the posterior oesophagus is similar to that of the anterior oesophagus, but the red staining gland cells seen only in the dorsal folds of the latter are scattered throughout the posterior oesophagus along with yellow staining gland cells and occasional mucous cells. The ciliated cells are about 50 μ high on the ridges and a little shorter in the grooves. Mucous cells are also more noticeable in the grooves and increase in numbers near the stomach. A coat of muscle (0.58 mm thick) surrounds the anterior part of the posterior oesophagus and is composed largely of mixed circular and longitudinal fibres, although there is a very thin layer of longitudinal fibres externally. Nearer the stomach the muscular coat becomes very thin and the overall diameter of the oesophagus increases from about 1.2 mm to about 2.2 mm.

The Stomach and Digestive Gland

The Stomach. The small, U-shaped stomach (Figs. 2, st., 12) is embedded in the digestive gland posteriorly and lies below the kidney dorso-anteriorly. It can be divided into 2 regions, the oesophageal half occupied by tall, ridged leaves and the intestinal half (i.a.) which has rather low, broad ridges, each half occupying its respective side of the U. The oesophagus (oes.) opens directly above the wide digestive gland aperture (d.g.o.). Emerging from this aperture below, and from the end of the oesophagus above, are about 10 tall leaves (st. pl.) sculptured with oblique secondary ridges, which run from the upper edge posteriorly downwards to the bottom of the groove between the folds.

Cilia on the outer edges of the leaves (Fig. 13) carry large particles towards the posterior extremity of the stomach (the base of the U) where they spill on to a small glandular pad (m.a.). Lighter waste particles fall off the apices of the leaves on to the secondary ridges (s.f.) where they are sorted as they are carried down between the leaves, only the smallest particles reaching the anteriorly flowing food current between the bases of the leaves. Ciliated tertiary folds (t.f.) tend to keep these smaller waste particles away from the bases of the secondary ridges so that they are kept in suspension and can thus be more efficiently sorted. The leaves are thus an efficient sorting device imposed upon an otherwise simplified stomach. They are kept relatively rigid by hydrostatic pressure as shown by the numerous arterial vessels and loose, spongy connective tissue in their interior. In the posterior region of the stomach, cilia drive particles towards the intestine along the tops of the folds, some of which are oriented obliquely on the floor; while in the grooves

of the lateral and dorsal folds the cilia carry the smallest particles back into the lumen of the stomach. This region is probably homologous with the style sac of other prosobranchs, as suggested by the 2 sets of oblique folds with a median groove between them, and by its general topography. There is no gastric shield or cuticle-lined area.

The histology of the anterior region of the stomach is essentially the same as that of the anterior and posterior oesophagus. The columnar ciliated cells have the same peculiar granular cytoplasm and large central nuclei, and they range from 20–65 μ in height. Goblet mucous cells are clustered on the apices of the outer ridges but are scarce throughout the rest of the epithelium. A few small, bluish staining subepithelial cells occur beneath the epithelium of the leaves. Amoebocytes are not particularly common. The secondary folds have a connective tissue axis whereas the tertiary ridges are formed by the variation in height of the epithelium.

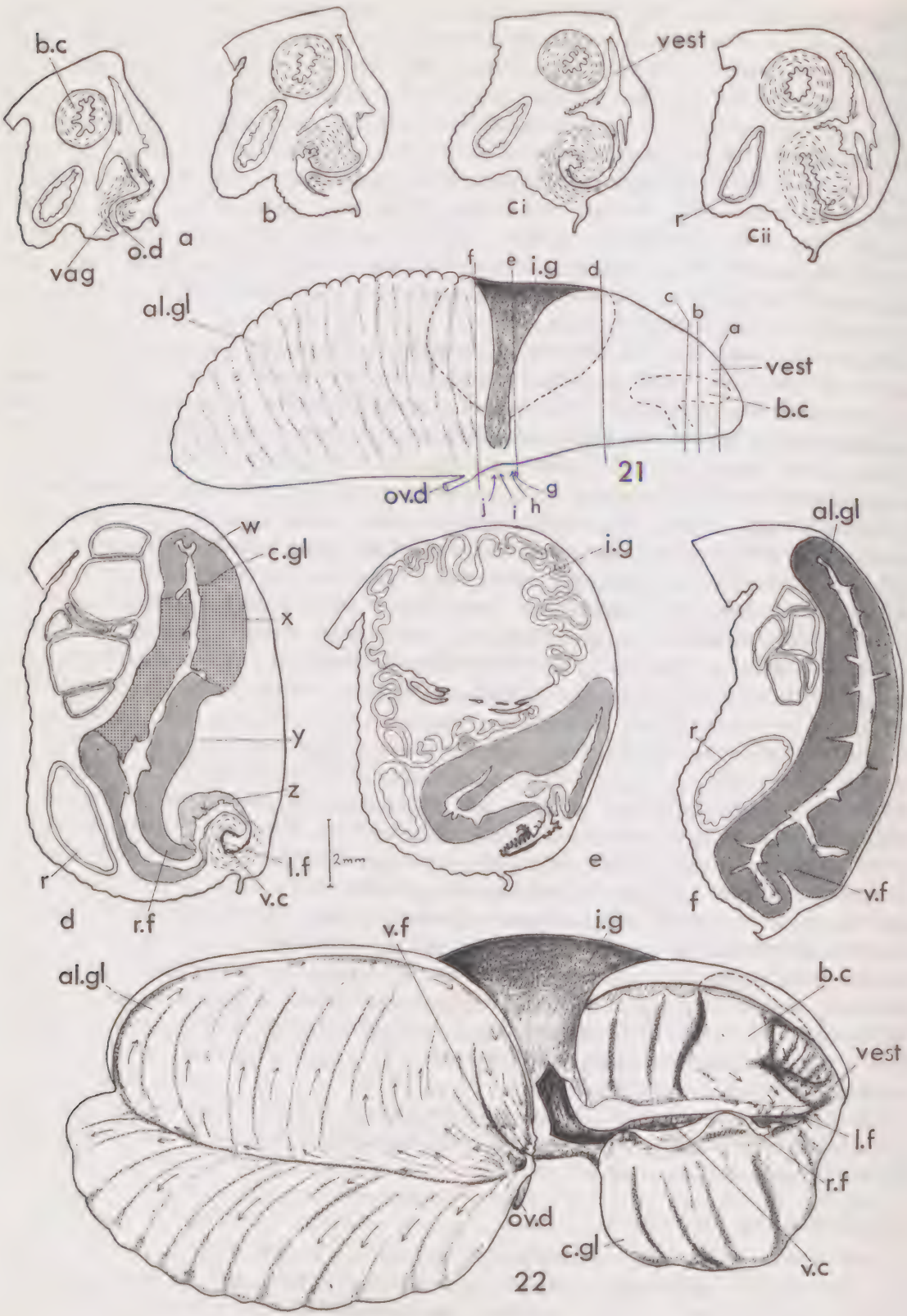
The intestinal region of the stomach has a taller epithelium (50–80 μ) than the anterior section and the cells have short cilia and basal or near basal nuclei. The cytoplasm in these cells is finely granular but it is not as dense as that in the epithelial cells of the oesophagus or in the anterior region of the stomach. Bluish, finely granular subepithelial cells are fairly abundant in the folds which also contain loose connective tissue, muscle fibres and occasional blood spaces. Mucous cells are scattered throughout the epithelium which is generally more opaque in life than that of the anterior region. A thin wall of mixed muscle and connective tissue between 30 and 50 μ thick surrounds the stomach.

The Digestive Gland. The single duct of the digestive gland (Fig. 12, d.g.d.) divides into 5 or 6 tributory ducts which in turn branch again and enter the digestive gland tubules. The heavily folded wall of the main duct is a continuation of the oesophageal end of the stomach but does not contain gland cells. Ciliary movements in the duct carry the fine food particles from the stomach into the digestive gland tubules. The cells in the main ducts range from 40 to 60μ in height though they are a little shorter in the collecting ducts. The digestive gland is composed of a mass of tubules, each lined with tall cells (Fig. 19) between 90 and 130 μ in height. These have basal nuclei, bluish staining, finely granular cytoplasm and contain a mass of large, red staining granules, though the distal quarter of the cells are usually free of these. Many cells have long cilia, and these are especially well developed on the 'young' cells while the larger cells often have irregular borders, are non-ciliated and are often actively ingesting food. Each tubule is surrounded by a very thin layer of connective tissue and is generally between 140 and 180 μ in diameter. Blood vessels are located between the tubules and are embedded in loose connective tissue. In some areas, especially around the blood vessels, amoebocytes (am.) aggregate together. These cells often store greenish-black staining granules in their cytoplasm and an abundance of these cells in an individual often coincides with a reduction in the secretory activity of the gland. In life the cells are pale yellowish-brown but the individual granules appear transparent and very pale yellow.

Only a trace of the primitive bilobed nature of the gland remains; the vestigial right lobe, which lies just below and to the right of the oesophagus, is separated from the massive left lobe by only a thin partition.

The Intestine and Anal Gland

The Intestine. After the intestine leaves the stomach it curves below the kidney and then runs along the right pallial wall where it terminates a little behind the exhalant opening of the pallial cavity. A short, triangular papilla, which is a continuation of the free edge of the rectum, lies above the anus.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The intestinal epithelium is folded into rounded ridges in the upper intestine and these subdivide in the rectum to form many low ridges. The intestinal epithelium is very tall (up to 130 μ high) with the cells containing central nuclei and very long cilia which reach a length of about 75μ. A very thin layer of circular muscle surrounds the intestine and there are a few longitudinal fibres below the epithelium. The rectal epithelium is like that of the intestine, but contains abundant mucous cells, the secretion of which binds the faecal material into pellets. The ciliated cells are shorter (50–100 μ), although the cilia are still very long. The rectum is surrounded by many small blood spaces which make up the rectal sinus. Near the anus the rectal epithelium is thrown into high folds which all but fill the lumen when it is empty. Here the columnar cells are still shorter and only a few mucous cells occur.

The Anal Gland. In life the anal gland is a black, diffuse mass which can be seen overlying the rectum and gonoduct in the antero-dorsal part of the right side of the pallial cavity. It has been shown to be excretory (Fretter, 1946), discharging material brought by amoebocytes from the digestive gland into the rectum. The pale staining cells of the anal gland (Fig. 20) have a pinkish-blue, finely granular cytoplasm and a large, spherical nucleus. Their distal ends often bulge into the lumen of the tubules which make up the gland. The cells are rather irregular in height (25–50 μ) and dark greenish refringent granules accumulate in their distal ends which are eventually nipped off, the buds forming spherules. Most of the epithelium is made up of non-budding ciliated cells, although these cells still contain the greenish granules that are seen in the mature cells. Numerous amoebocytes are located in the connective tissue between the tubules and there are abundant blood spaces. The short duct of the anal gland is an outgrowth of the rectum as it is lined with rectal epithelium, and it opens a little behind the anus.

Fretter (1946) found that all of the cells of the anal gland in *Nucella lapillus* were ciliated, but Smith (1967) has shown that in those rachiglossans and Turridae that he examined, only the duct of the gland is ciliated.

THE GENITAL SYSTEM

The Female Genital Tract

Although the female genital tract of *Alcithoe* (Figs. 21, 22, 23) resembles in general plan that of the rachiglossans described by Fretter (1941), it differs in several important details.

The Ovary. A small series of brownish tubules thinly spread on the inner-dorsal surface of the digestive gland make up the ovary. The small ova are reddish-brown when mature and are only 200 μ in diameter. They break away from the cuboidal germinal epithelium when about 50 μ in diameter and develop free within the tubules. A thin-walled, trans-

FIG. 21. Right lateral view of the glandular oviduct. The lines and arrows (a-j) indicate the levels of transverse sections 21 a-f and 23 g-j. The section in Fig. 21 ci is slightly anterior to that in 21 cii. (*a*) Section through vestibule, vagina, bursa copulatrix, and female opening. (*b*) Section through vestibule just behind female opening. (ci, cii) Sections through bursa copulatrix and base of its duct. (*d*) Section through capsule gland and part of the ingesting gland. (*e*) Section through ingesting gland and posterior end of capsule gland. (f) Section through the anterior portion of the albumen gland. FIG. 22. The glandular oviduct opened to show the ciliary currents. Arrows indicate ciliary currents.

al.gl., albumen gland; b.c., bursa copulatrix; c.gl., capsule gland; i.g., ingesting gland; l.f., left fold; o.d., external aperture of oviduct; ov.d., oviduct; r., rectum; r.f., right fold; vag., vagina; v.c., ventral channel; vest., vestibule; v.f., ventral fold of albumen gland; w, x, y, z, Glandular regions of capsule gland (see text).

parent oviduct (ov.d.) about 250 μ wide passes just below the pericardium. The epithelium thickens at this point, but there is no renopericardial duct, either functional or vestigial. The oviduct is lined with loosely packed, non-staining columnar cells with central nuclei and is surrounded by a few muscle fibres. The ova presumably move along this tube by peristalsis, as there are no cilia. Towards the entry of the oviduct into the albumen gland just behind the opening of the albumen gland duct, its epithelium becomes cuboidal and ciliated, and the walls are surrounded by a muscular sphincter.

The Albumen Gland. In Fleure's (1912) description of the female genital tract of *Cymbium*, the albumen gland has apparently been mistaken for the ovary, the upper edge of this gland being crenulated so that it looks superficially tubular.

The mature albumen gland (al.gl.) in *Alcithoe* is about 2 cm long and in contrast with the condition in most Stenoglossa, the segment comprising the capsule gland and vestibule is only about half as long. In life the glandular walls of the albumen gland are creamy-white whereas those of the capsule gland are dirty-white. Weak, opaque folds run ventrally backwards on the interior of the lateral lobes of the albumen gland, whereas at the anterior end where the 2 openings lie close together antero-ventrally, ridges and grooves radiate from the openings. The upper opening leads to the ventral channel of the capsule gland whereas the lower opens into the oviduct. The ova are carried by ciliary currents from the oviduct along the ventral part of the outer side of a fold (v.f.) lying between the 2 openings. They are surrounded by albumen as they are passed upwards to the dorsal groove lying between the 2 closely contiguous lateral walls.

The epithelium of the albumen gland is composed of multicellular alveoli and is thus similar to that of the rachiglossans described by Fretter (1941). There is, however, only one type of gland cell throughout most of the gland and this has minute dark staining granules and a distinct red staining basal nucleus. Small, wedge-shaped ciliated cells occur over the surface of the glandular lobes. In the antero-ventral region between the 2 openings of the gland the gland cells stain purplish-red, but these are otherwise identical in structure with the other gland cells, some of which are intermingled with them. A few epithelial goblet cells also occur in this region. Externally, the gland is surrounded by a very thin sheath of connective tissue.

The albumen gland appears not only to have become arched as in *Nucella*, but to have fused and become continuous along its 2 inner faces. Thus the ventral groove behind the opening of the oviduct is equivalent to the posterior half of the original dorsal groove and the original ventral surface has all but disappeared.

The short duct from the albumen gland (al.d.) opens into the base of the duct of the ingesting gland which is brownish and conspicuously ridged. The duct is continuous with the closed posterior part of the ventral channel of the capsule gland (Fig. 23g-i, v.c.). The walls of these ducts are surrounded by a thick layer of transverse muscle (Fig. 23g-j).

The duct of the albumen gland (al.d.) is merely a continuation of the postero-ventral part of the gland from which it is derived. Its walls are folded and covered at the proximal end with the same tall gland cells that line the ventral part of the albumen gland itself. The first part of the inner wall possesses some multicellular alveoli, but the other walls are made up of single layers of cells. Mucous cells are especially abundant on the thin ventral wall, but on the outer lateral walls they are less common and are mixed with red and blue staining gland cells. Dorsally the mucous cells are only sparse and the epithelium is composed largely of non-glandular, columnar, ciliated cells as well as a few albumenous cells. At the anterior end of the duct the gland cells are scarce and the lumen is much smaller. The ventral epithelial cells are filled with very dense granular, orange-red staining

FIG. 23. (*g*) Section through duct of capsule gland at its proximal end. (*h*) Same a little further posteriorly. (*i*) Section through capsule gland duct showing separate ciliated portion (albumen gland duct) and a portion of the duct of the ingesting gland. (*j*) Section through ingesting gland and its duct. FIG. 24. Cells lining wall of ingesting gland near its duct. FIG. 25. Ingesting gland cells showing cycle of ingestion. FIG. 26. Transverse section of accessory seminal receptacle. FIG. 27. Cells from posterior region of bursa copulatrix. FIG. 28. Cells from crests of ridges just in front of opening of bursal duct in mid-ventral area of bursa copulatrix.

al.d., albumen gland duct; a.s.r., accessory seminal receptacle; i.g., ingesting gland; r., rectum; sp., sperm; v.c., capsule gland duct.

cytoplasm, and these are continuous with identical cells in the ciliated part of the ventral channel. The dorsal channel is minutely folded, and below this, a pair of broad, lateral folds contain remnants of the albumen gland epithelium.

The Ingesting Gland. The ingesting gland (i.g.) is situated between the albumen and capsule glands and lies on the right side of the pallial oviduct. It is conspicuous in life owing to its dark brown colour imparted by the cells lining the gland. The interior is subdivided into tubules and pockets containing white masses of immobile, and possibly

dead, spermatozoa. The fluid in the lumen is a mixture of dark brown and pale brown viscous secretions, the colour varying with the relative amounts of the brown secretory granules liberated by the epithelial cells. The fluid itself stains blue like the secretion from the albumen gland. Most of the gland is lined with columnar cells ranging from 80–210 μ in height (Fig. 25). These cells contain brownish-yellow secretory granules which appear pale-yellowish when stained and their nuclei are large and basal. They appear to have a double function. Most of them liberate the brown granules referred to above but many have vacuoles containing brownish, amorphous masses, probably the products of sperm breakdown after ingestion (Fretter, 1941). Occasional cells have been observed ingesting sperm, which can sometimes be seen in the vacuoles. Several vacuoles in each cell ultimately coalesce and liberate their contents into the lumen (Fig. 25).

Sperm ingestion does not appear to be very common even though the gland was often packed with sperm. Possibly the secretion from the majority of the glandular epithelium causes extracellular breakdown, though this could not be demonstrated in sectioned or living material. Fresh sperm left in the fluid of the lumen was still intact, though immobile, after 15 hours. Thus external breakdown, if it occurs at all under artificial conditions, must be very slow.

The lower 1/3 of the gland (Fig. 23j) has a cuboidal epithelium, the cells being only 25–30 μ high and covered with a soft cuticle (Fig. 24). This area is sharply separated from the glandular area and partially cut off from it by an incomplete septum. The cuboidal cells near the glandular epithelium often have small, black, refringent granules in their cytoplasm and they sometimes also contain 1 or 2 large, red staining granules. Their nuclei are large and round and each has a central nucleolus. The ingesting gland duct, and the area of cuboidal epithelium near it, have very complexly folded surfaces on which sperm temporarily accumulate. The cuboidal cells in both these areas are similar, but in the duct they have very dense, granular cytoplasm which stains orange-red like that in the cells of the ventral channel of the capsule gland.

The Capsule Gland Duct. The ingesting gland duct is formed from the posterior continuation of the ventral channel of the capsule gland. The ciliated duct of the albumen gland joins the non-ciliated duct of the capsule gland in front of the ingesting gland duct (Fig. 23h) and continues as a ciliated outer arm as far as the base of the capsule gland (Fig. 23g). The capsule gland duct consists of 4 main grooves. The dorsal, ventral and inner grooves are lined by a non-ciliated, cuboidal epithelium like that of the ingesting gland duct, and are produced into secondary and some tertiary grooves. The outer groove is the ciliated arm referred to above. Its outer-most wall contains mucous goblet cells, the inner walls being lined with red staining cells of similar size to those of the rest of the duct. The whole duct is surrounded by a coat of transverse muscle.

The Accessory Seminal Receptacles. Several narrow tubes emerge from the dorsal channel of the albumen gland duct (Figs. 23h-j, a.s.r.), the anterior end of the albumen gland just above its duct, and the ciliated outer groove of the albumen duct from the ingesting gland duct. These are generally lined with ciliated cuboidal or short columnar epithelium 30–40 μ high proximally, but more elongate distally. The proximal parts of the tubules are surrounded by the muscular coat of the structures from which they arose (Fig. 26), but the upper parts are not muscular. Distally the epithelial cells lengthen to about 80 μ, lose their cilia and become filled with pale yellowish-brown granules like those seen in the ingesting gland cells. The tubules coalesce distally into one or a pair of sacs near the outer wall of the ingesting gland (Fig. 23j), and these eventually become confluent with this gland. The tubules that arise from the albumen gland and its duct

contain small amounts of albumen. The others contain varying quantities of sperm, which is usually attached to the epithelium in the middle sections, although loose bundles are sometimes present in their lower parts (Fig. 26). The proximal parts of the tubules that arise from the ingesting gland duct are lined with the same non-ciliated epithelium as that of the duct.

The Capsule Gland and Vestibule. The capsule gland (Figs. 21, 22, cap.), together with the vestibule (vest.), forms a relatively short segment of the oviduct in *Alcithoe*, which therefore differs from all other described Neogastropoda. When this anterior segment is opened dorsally a massive fold on the right (r.f.) can be seen to overlie a ventral channel (v.c.) along all but the extreme anterior and posterior ends. Below this fold a rounded ridge protrudes on the left (l.f.) and the long fold closely overlaps this to form an enclosed canal. At the posterior end of the segment the right fold disappears and the left enlarges to completely enclose the ventral channel by fusing with the right wall. The glandular lobes of the capsule gland occupy approximately the posterior 2/3 of the lateral walls of the anterior segment of the oviduct. The vestibule lies in front of the duct to the bursa copulatrix (Fig. 22, vest.) to form the anterior-most part of the oviduct.

Ciliary currents could not be determined on the main glandular lobes of the posterior half of the capsule gland, though short cilia are present. Thin sheets of capsular secretion are extruded over the surface of the gland as soon as the existing layers are removed. These harden slightly on contact with seawater and can be removed in their entirety. The thinner walls in the anterior part of the capsule gland, and the vestibule, have the currents directed ventrally into the opening of the bursa copulatrix just in front of it and, also, towards the external female aperture (Fig. 22). No ciliary currents could be observed on the right lateral wall of the ventral channel, though cilia were detected in sections in that area. On the left fold, however, cilia beat downwards into the lumen of the channel on its dorsal and ventro-lateral surfaces.

The glandular lobes of the capsule gland have a similar histology to those described by Fretter (1941) for *Nucella*. These are multi-cellular alveoli with a layer of epithelial gland cells and ciliated cells on the surface of the lobes. The gland cells show 3 types of staining, but these are not as clear-cut as they are in *Nucella*. Anteriorly pale-red staining cells occur on the upper 1/3 of the right lobe and on the upper 2/3 of the left (Fig. 21d, x) continuing further back only on the left. There is an area of blue staining cells in the mid-dorsal region between the lobes (Fig. 21d, w) and also on the rest of the lateral walls (Fig. 21d, y). In the anterior region of the capsule gland there is a narrow, mid-dorsal strip of cells containing pale blue to colourless granules. Below the right fold and above the left is a zone of spongy gland cells (Fig. 21d, z), some containing pale blue granules in their 1st stage of secretion, but the majority have colourless vacuoles. Although this epithelium is structurally similar to the rest of the glandular tissue, the alveoli have much wider lumina and the gland cells are shorter. This zone is poorly represented at the anterior end of the capsule gland, but it is well developed through the rest of the gland.

The External Aperture, Ventral Channel and Bursa Copulatrix. The organs for receiving and conducting sperm, though essentially one unit, consists of 3 parts, the external aperture (o.d.), the ventral channel (v.c.) and the bursa copulatrix (b.c.). The ventral channel opens into the mantle cavity a little behind the anterior limit of the vestibule (Fig. 21a, o.d.). Above and behind this external opening is the aperture of the bursa copulatrix (Fig. 21, ci, cii). The large quantities of sperm sometimes contained in the bursa appear to be deposited directly by the penis. After copulation the spermatozoa

are moved, probably largely by peristalsis, along the ventral channel to the ingesting gland. Fertilization probably occurs in the duct of the capsule gland or in the albumen gland. The external aperture of the oviduct is a short, ventral slit which is practically closed off by the muscular left lobe of the ventral channel, from the ventral channel. The right lobe is represented by a slight bulge only. The vagina is very short, this name being applicable to that part of the walls of the oviduct between the lips of the opening and the distal edge of the left fold. A few, large, goblet cells up to 40 μ across are found in its distal parts where the ciliated cells reach a height of about 85 μ. The ciliated epithelial cells lining the rest of the vagina have central nuclei and dense cytoplasmic granules that stain orange-red. The epithelium of the inner part of the vagina is relatively thinner (about 35 μ) and the cells contain denser cytoplasmic granules. The external lips are very muscular and their lubrication during copulation is provided by a modified area of the hypobranchial gland. The gland cells surrounding the lips are short (129–160 μ high) compared with those of the hypobranchial gland proper (250 μ), and only mucous and ciliated cells are present. The epithelium just inside the lips described above, is a transition zone between this outer area and the vagina.

Behind the external opening lies the ventral channel. This structure is surrounded by a thick layer of muscle fibres which are mainly longitudinal. It runs the length of the capsule gland and transports sperm by peristalsis to the ingesting gland. The epithelium initially is the same as that of the inner vaginal area, but opposite the opening of the bursa copulatrix the cilia are lost and are replaced by a soft cuticle-like layer in which the heads of spermatozoa are often embedded. The dense cytoplasmic granules of these cells stain purple-red and on the ventral surface and parts of the dorsal surface of the channel they form multi-cellular glandular masses which reach a thickness of up to 150 μ. However, over most of the dorsal surface, this epithelium is a single layer of cuboidal cells only 10 μ high. The outer part of the groove (that is the distal end of the left fold and the immediate ventral portion together with the section of the outer wall opposite) is lined with cells similar to those of the ventral channel except that they are ciliated.

The right fold of the capsule gland that encloses the ventral channel is presumably homologous to the anterior ventral lobe described by Fretter (1941) in *Nucella* while the left fold represents the left longitudinal fold of that species. The right longitudinal fold (in *Nucella*) appears to be missing in *Alcithoe* and in the larger Toxoglossa(Martoja-Pierson, 1958; Marcus & Marcus, 1960). The right fold terminates near the posterior end of the capsule gland and at this point the musculature and size of the left fold increases considerably. The red staining glandular epithelium is reduced to little more than a layer of cuboidal cells over most of the now heavily folded surface, and small, blue staining subepithelial cells occur below them. With the coalescing of the left fold with the right side of the ventral channel (Fig. 21e) the enclosed posterior duct of the capsule gland is formed.

The bursa copulatrix (b.c.) is a diverticulum of the ventral channel as it represents an anterior continuation of the innermost portion of the ventral channel. This has been segregated by the left fold arching over to meet the left wall below its own base (Figs. 21a-c). The duct, although nearly vertical, is a little posteriorly inclined. At its distal end it bulges posteriorly into a very short swelling and anteriorly into a longer diverticulum which extends almost to the anterior end of the pallial oviduct. The lumen is often empty which suggests that the bursa is only a transitory sperm storage organ emptied soon after copulation. Only unorientated sperm have been observed in the bursa, as in *Olivancillaria (Lintricula) auricularia* (Lam.) (Marcus & Marcus, 1959).

A thick coat of muscle fibres varying in orientation surrounds the bursa. The epithelium is thrown into about 9 folds which are underlain by loose connective tissue containing some muscle fibres. In front of the bursal opening the ventral channel is ciliated and there are small mucous cells on its ventral surface. These cells continue along the posterior wall of the 1st part of the bursal duct and their secretion presumably aids the passage of the penis during copulation. The upper wall of the proximal bursal duct is lined with a ciliated columnar epithelium about 65 μ in height. The cells contain rather narrow nuclei that vary from basal to central in position. Yellow granules in small vacuoles are scattered through the finely granular cytoplasm which stains dense pinkish-red. Ventrally the ciliated supporting cells are similar in structure, but the cytoplasm has no granular secretion and is less dense. In the middle part of the bursal duct is a zone of orange staining, very tall and narrow gland cells between 50 and 100 μ in height These liberate large, oval, orange granules into the lumen of the duct and their nuclei are minute and basal in position. Patches of this epithelium on the folds are ciliated, though their cytoplasm appears to be identical to that of actively secreting cells. In between the folds these cells tend to be covered with a cuticle-like layer similar to that seen in the ventral channel. In the initial horizontal part of the bursa near the duct the cells resemble those of the lower bursal duct, though those in the ventral area anterior to the duct have smaller and denser nuclei. These cells are generally about 40 μ high, have a cuticularized surface, and line the grooves between the ridges in this part of the duct. The crests of the ridges are capped with tall cells having bluish-purple instead of reddish-purple staining cytoplasm, which is highly vacuolate (Fig. 28). The distal ends of these cells have short cilia, except for those which are actively discharging. dorsally, in this initial anterior region, the cells resemble those of the posterior bulge of the bursa. They are columnar (80-130 μ tall), with large nuclei. They are, however, shortly ciliated in the posterior parts of the bursa (Fig. 27), but covered with a thin cuticle anteriorly. Their cytoplasm stains bluish and is slightly vacuolate. Anteriorly the epithelium is uniform, the long, narrow cells in this region being between 50 and 120 μ in height. They are covered with a distinct cuticle and have a bluish-purple staining cytoplasm. These cells are continuous with the epithelium on the crests of the ridges nearer the duct. Occasional amoebocytes occur in the loose connective tissue below the epithelium.

The Ventral Pedal Gland. The ventral pedal gland of the female is an oval depression about 1.25 cm in width which is situated a little behind the anterior edge of the sole. It is readily distinguished from the rest of the sole by its denser white colour and heavily folded appearance. The glandular tissue is a uniform mass of subepithelial cells, each about 20 μ in diameter. Their cytoplasm is packed with small pinkish granules which are liberated through long ducts that penetrate the pedal epithelium. A few radial muscle fibres run through the gland. The pedal epithelium covering the gland has fewer mucous cells than the rest of the sole and it is thrown into folds which increase the surface area.

The Egg Capsule and Oviposition. The egg capsule and embryonic shell of *Alcithoe* have been described by Suter (1919) and Graham (1941a). Oviposition has been observed throughout most of the year, but capsules are most commonly encountered in spring and summer. The capsules are solitary, hemispherical or nearly subspherical and between 10 and 15 mm in diameter. They are deposited on objects of suitable size for the animal to grip with its foot, such as dead mollusc shells, pebbles or pieces of water-logged wood. The animal usually oviposits at the surface or while only slightly buried and has every resemblance to a feeding individual. The object, with the egg capsule placed on top,

is held tightly by the foot while a thin, porus, calcareous layer is secreted over the horny capsule by the ventral pedal gland. This layer is at first rather flexible but soon hardens and provides some protection for the delicate capsule that lies beneath it.

The capsule contains a mass of pale blue staining secretion identical to that of that albumen gland, while the membranous capsular layer has similar staining properties to the secretion from the capsule gland. The capsule consists of 3 layers, an outer and an inner purplish-red staining layer and a middle layer that stains pale purplish-blue. The outer layer is about 15–20 μ thick. The middle is usually between 35–90 μ but is sometimes thicker and the inner layer is about 25 to 35 μ thick. The capsule adheres firmly to the object on which it rests and in addition the calcareous layer is also cemented to this object. The albumen secretion is pure white in life, very finely granular, stiff and coherent.

The number of ova in a freshly laid capsule could not be determined because of their exceedingly small size and the large quantities of albumen present. Because the capsule is large and solitary and the ova are small it is probable that a large number of ova are incorporated. If this is the case, embryonic cannibalism must reduce the numbers, as has been observed in several Stenoglossa (Fretter, 1941) since only 1 to 3 embryos emerge (Suter, 1919; Graham, 1941a). These hatch as crawling, operculated animals 5 mm long (Graham). The capsules are figured by Graham (pl. 23, figs. 9a, 9b) and the embryonic shell by Suter (1919, p 74).

The Male Genital Tract

The Testis. The mustard-yellow testis (Figs. 2, 29; tes.) is much larger than the ovary and occupies the left (outer) portion of the visceral coil. It consists of a mass of tubules, each being about 300 μ in diameter and encased in a thin tunic of connective tissue. There are no atypical sperm, all spermatozoa having normal pointed heads and flagella between 100 and 200 μ in length.

The Vas Deferens. A brown mass of short, branching acini emerge a little behind the anterior limit of the testis and terminate at the edge of the pericardium. This section of the vas deferens (s.v.) is homologous with the coiled seminal vesicle of other Stenoglossa, being lined with a pavement epithelium about 5 μ high. Its cytoplasm contains vacuoles, some of which are filled with concretion-like aggregations of greenish-yellow granules. Some of the tubules, particularly the outer ones, also have small greenish-yellow granules in the otherwise colourless cytoplasm. These granules are brown in life and give the seminal vesicle its conspicuous colour. Occasional amoebocytes of unknown function and of similar structure to the epithelial cells, and others that stain darker purplish-red, occur between the tubules.

The yellowish concretions of the seminal vesicle epithelium appear to be similar to those described by Linke (1933) in *Littorina* and Fretter (1941) in the Rachiglossa as the supposed products of sperm breakdown after ingestion by the epithelial cells. Similar concretions have been observed by Marcus & Marcus (1959) in *Oliva sayana* Ravenel and by the same authors (1962) in *Leucozonia nassa* (Gmelin), although no sperm ingestion was noted in these species. Neither was it observed in the rest of the Olividae studied by Marcus & Marcus (1959) nor in the Columbellidae (Marcus & Marcus, 1962a). In the present study no definite indication of sperm ingestion was observed in *Alcithoe*, even though the tubules were often packed with sperm.

The renal section of the vas deferens traverses the pericardium (pc.) in the same manner as the equivalent female duct and there is no trace of a gono-pericardial canal. This duct is about 0.4 mm in diameter and is separated from the pericardium (pc.) only by

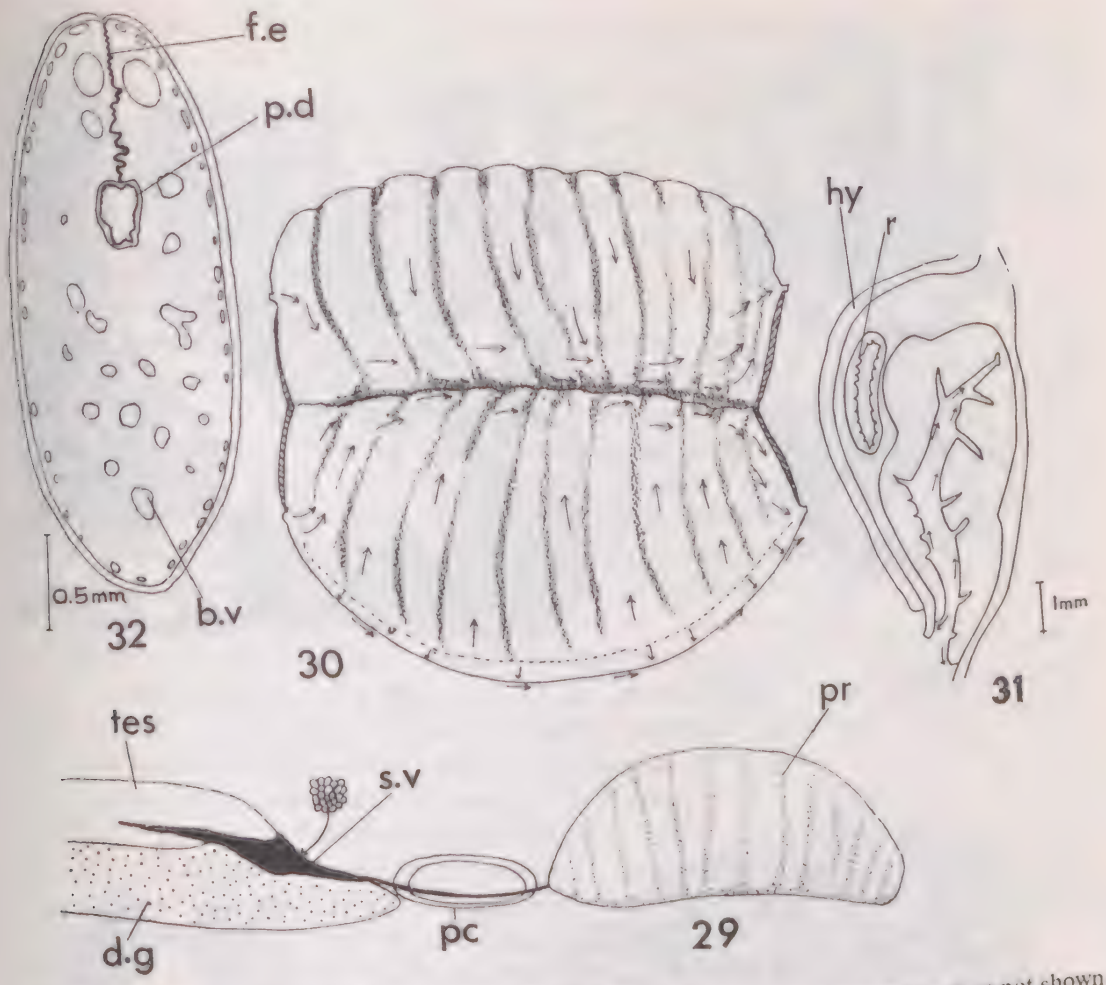


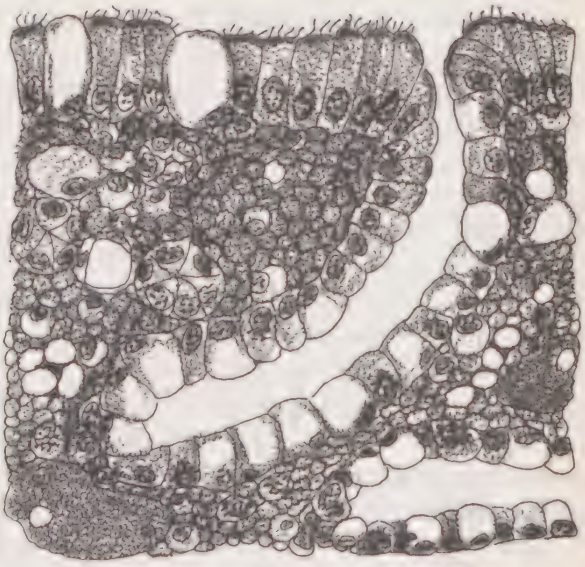
FIG. 29. Right lateral view of male system as seen externally. Penis and ejaculatory duct not shown. FIG. 30. Prostate opened dorsally to show the ciliary currents. FIG. 31. Transverse section through middle of prostate gland. FIG. 32. Transverse section through middle of penis. Arrows indicate ciliary currents.

b.v., blood vessel; d.g., digestive gland; f.e., fused epithelium; hy., hypobranchial gland; pc., pericardium; p.d., penial duct; pr., prostate; r., rectum; s.v., seminal vesicle; tes., testis.

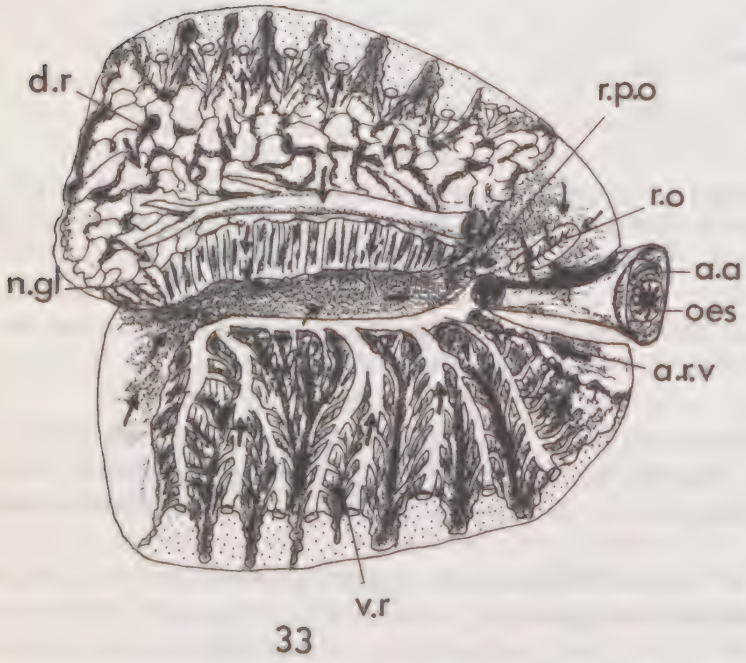
a thin layer of muscle and connective tissue. The ciliated epithelium is variable in height and forms longitudinal ridges, the cells having weakly staining contents and central nuclei. A thin layer of muscle surrounds the duct, but this is barely distinct from that of the body wall.

The Prostate Gland. Just in front of the pericardium at the base of the mantle cavity, the vas deferens opens into the prostate gland (pr.), a massive, oval structure lying along, the right side of the mantle cavity. Spermatozoa are swept by cilia into the dorsal groove between the 2 lateral glandular lobes of the prostate, where they are passed forwards (Fig. 30). Dorsally beating cilia drive the prostatic secretion liberated by the gland into the dorsal groove where it mixes with the spermatozoa. The ventral margin of the gland is open to the mantle cavity along all but its most posterior portion (Fig. 31). Rejection cilia prevent extraneous particles from entering between the loosely applied ventral lips. The glandular walls of the prostate consists of multicellular bundles up to 2 mm thick.

35 10 μ



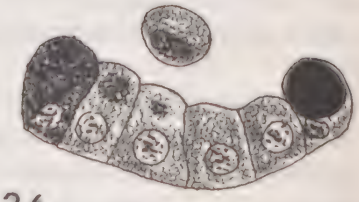
34 20 μ



33

5 μ

37



36 5 μ

FIG. 33. Renal organ opened dorsally to show its structure and ciliary currents. FIG. 34. Cytology of the dorsal renal glandular mass. FIG. 35. Cytology of the ventral renal glandular mass. FIG. 36. Cells of the nephridial gland. FIG. 37. Epithelial cells from the renal canals that penetrate the nephridial gland. Arrows indicate ciliary currents.

The cells are filled with red staining granules and their long distal ends penetrate the ciliated columnar epithelium covering the glandular surface. The ciliated cells, which also contain red granules, together with a single layer of short gland cells, form the epithelium on the inner-most part of the lips of the prostate, while only the ciliated cells are found at their outer-most tips. This situation is comparable with that observed by Fretter (1941) in *Ocenebra erinacea* (L.) where 2 layers of epithelium, continuous with that of the ciliated epithelium of the glandular surface, indicate where the lips of the prostate have fused.

The Ejaculatory Duct. The short, straight ejaculatory duct emerges from the anterior end of the prostate. It is about 0.6 mm in diameter and the ciliated epithelium forms longitudinal ridges that impinge on the rather wide lumen. The epithelial cells of this duct are like those of the renal vas deferens. A narrow layer of circular muscle fibres surrounds the duct, although it is barely differentiated from the thick muscular tissue in which the duct is buried. An irregular double strip of cuboidal cells extends from the duct to the surface of the mantle cavity, this representing a fused ventral slit. At the junction of this strip with the surface a break in the outer epithelium forming a shallow groove can be observed. This groove and strip are continuous with those of the penial duct (Fig. 32; f.e.).

The Penis. The penis (Fig. 2; pen.) is rather short, being about 15 mm long when retracted, and is usually reflected back into the mantle cavity. It is rather flattened and the distal half, which is about 6 mm wide and 2 mm thick, is broader than the proximal half. The small, slit-like penial opening is situated terminally. The epithelium is pigmented in the same manner as the rest of the dorsal parts of the head-foot. The penial duct (p.d.) is similar to the ejaculatory duct, although it is not surrounded by a muscular coat. A cuticle covered epithelium, which contains numerous mucous cells, covers the penis, and the interior is filled with longitudinal and transverse muscle fibres, amongst which are numerous blood vessels (Fig. 32). The penis of *Olivancillaria (Lintricula) auricularia* is very similar in structure (Marcus & Marcus, 1959).

THE RENAL ORGAN

The renal organ of *Alcithoe* is an oval sac similar to that of *Olivancillaria* (*Lintricula*) *auricularia* (Marcus & Marcus, 1959), *Cymbium melo* (Fleure, 1912), and *Cymba pepo* (Perrier, 1889).

A membraneous sheet separates the renal organ from the pericardium on the left and from the mantle cavity in front, and it bulges over the intestinal end of the stomach behind. Externally (Fig. 2) the renal organ consists of 3 sections: an orange-brown section in the middle (d.r.); a pinkish-brown mass, the nephridial gland (n.gl.), on the left bordering the pericardium; and a dark brown portion on the right (v.r.), which also occupies the whole floor of the sac. The afferent renal vein emerges from the floor of the renal organ (Fig. 33, a.r.v.) and gives rise to 2 branches. The ventral branch gives off a series of vessels which supply the ventral glandular mass which is arranged in parallel lamellae, and the other branch supplies the irregular dorsal glandular mass on the posterior and right hand roof of the kidney. The dorsal branch of the renal vessel partially divides

a.a., anterior aorta; a.r.v., afferent renal vein; d.r., dorsal renal glandular mass; n.gl., nephridial gland; oes., oesophagus; r.o., renal opening; r.p.o., reno-pericardial opening; v.r., ventral renal glandular mass.

the renal lumen into an anterior, thin-walled bladder and a posterior, glandular sac. Between the outer left wall and the dorsal glandular mass is the nephridial gland (n.gl.) which, in dissection, appears to be made up of vertical fibres with narrow, slit-like invaginations between them. Opening next to the base of the afferent renal vein is the tiny reno-pericardial pore (r.p.o.). The slit-like renal opening (r.o.) to the mantle cavity is situated in the middle of the anterior wall.

The cytology of the renal organ is essentially like that of *Buccinum* (Dakin, 1912). The ventral glandular tissue is predominantly composed of vacuolate cells which give it a honeycomb appearance in section (Fig. 35). The epithelium covering the surface of this part of the renal organ is composed of columnar cells, but those making up the internal glandular tubules are cuboidal when immature, and these eventually become distended by a large vacuole forming in the cytoplasm of each cell. Like all of the cells of the renal organ they have a large nucleus and pinkish-mauve cytoplasm. Amoebocytes containing refringent greenish staining granules occur in small pockets between the glandular tubules and blood vessels that permeate the ventral glandular tissue. Small, wedge-shaped, ciliated cells are lodged between the other epithelial cells and are especially common on the upper surface of the main ridges. They are also found intermittently throughout the ventral gland. Each cell in the outer epithelium contains several vacuoles and liberates its contents by budding off its distal end. This process is especially active on the main ridges.

The dorsal glandular tissue (Fig. 34) contains weakly ciliated, short columnar cells on its outer surface, these often being shorter than those shown in the figure. Large goblet cells are interspersed between the ciliated cells. The histology is complex; non-ciliated cuboidal cells, both vacuolate and non-vacuolate, line the internal tubules that make up the bulk of the dorsal gland and give it its spongy texture. The large nuclei are 1/3 to 1/2 the height of the cells, and some cells have clusters of refringent greenish staining granules surrounding their nuclei. The tissue between the tubules is frequently bulky and consists of masses of storage cells packed with minute purplish staining granules which often obscure the cell membranes and nuclei. Storage cells are found in especially dense clusters near the ventral (inner) edges of each fold. Similar cells have been observed in *Buccinum* (Dakin, 1912, p 339, pl. 7, fig. 53). The inner and dorsal parts of the folds have much wider tubules and therefore a looser structure. Some amoebocytic cells occur in the connective tissue and these sometimes contain refringent granules like those in some of the glandular cells.

The nephridial gland tissue resembles that of the rest of the renal organ. The cells (Fig. 36) are arranged in close-knit tubules which form a compact mass, and they accumulate greenish staining refringent granules to a much greater extent than cells in the rest of the renal organ. Goblet cells with uniform, orange to yellow staining contents occur intermittently amongst the normal epithelial cells. A few amoebocytes occur in the lumen of the tubules. Wide canals invaginated from the renal sac penetrate this gland. These are lined with taller columnar cells (Fig. 37) than in the rest of the gland and they are often seen budding off their distal ends, though there are no vacuoles or distinctive granules in their cytoplasm. The outer epithelium of the nephridial gland that lines the renal cavity is similar to that of the other outer lining cells.

The membraneous walls of the renal organ are lined with columnar or cuboidal cells which are either ciliated or vacuolate.

Ciliary currents on the surface of the renal organ are shown in Fig. 33. The general movement is towards the renal opening.

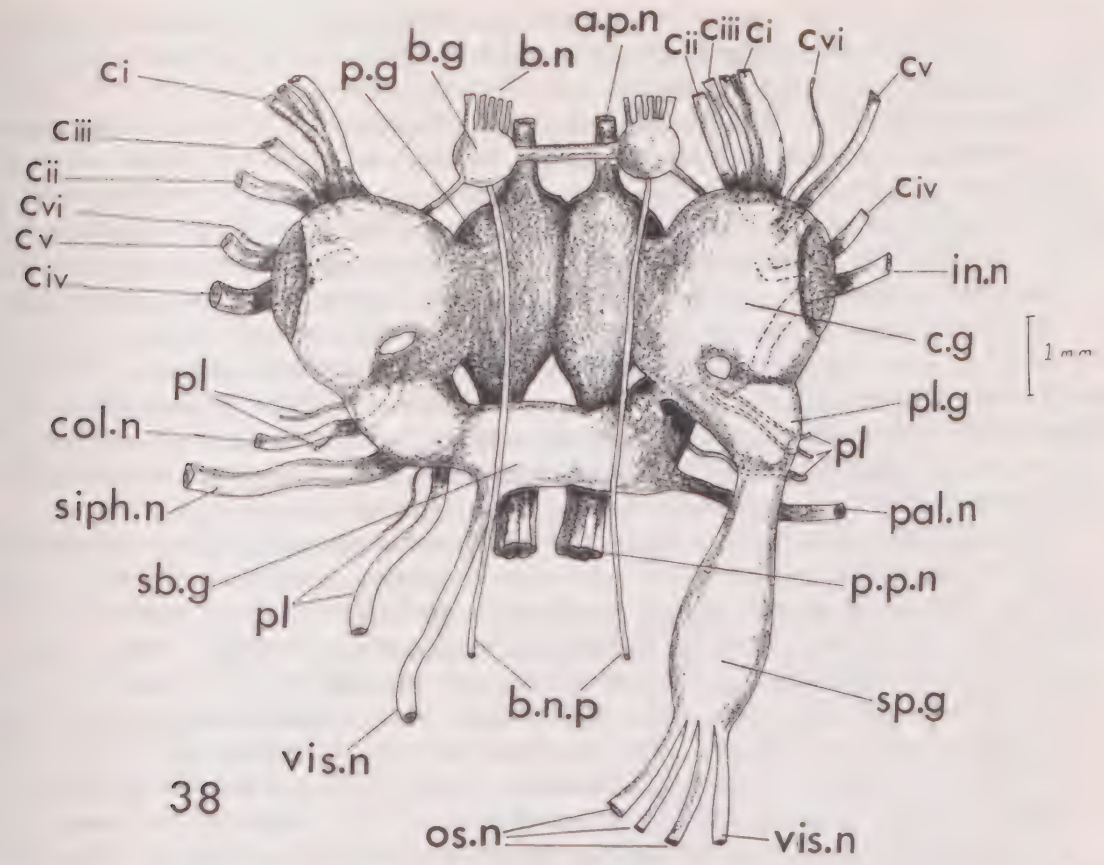


FIG. 38. Dorsal view of the circum-oesophageal ganglia and their nerves. The cerebral ganglia have been separated and spread laterally. For explanation of abbreviations see text.

THE NERVOUS SYSTEM

The central nervous systems of 7 species of the Volutidae have already been described. These are of 2 types, the 1st with the supra-intestinal and right pleural ganglia widely separated, and the 2nd with these 2 ganglia closely fused together. The 1st group includes *Hiala priamus* (Poirier, 1885), *Voluta musica* (Pace, 1902) and *Cymba pepo pepo* (Bouvier, 1887a), whereas the 2nd group includes *Cymbium melo* (Fleure, 1912), *Neptuneopsis gilchristi*, *Adelomelon ancilla*, *Voluticorbis abyssicola* (Woodward, 1900) and *Harpovoluta charcoti* (Eales, 1923). The nervous system of *Alcithoe* is one of the 2nd type and shows considerable concentration of all the circum-oesophageal ganglia.

The relative sizes of the ganglia can be seen in Fig. 38. The cerebral ganglia (c.g.) are large, with a very short, broad commissure and are attached by a short, wide connective to the pedal ganglia (p.g.) which lie below. The pleural ganglia (pl.g.) are fused to the cerebral ganglia, from which they are barely distinguishable. The elongate supra-oesophageal ganglion (sp.g.) lies on the dorsal surface of the oesophagus behind the cerebral ganglia, and it is attached to the left pleural ganglion by a short connective. Below the oesophagus is the large sub-oesophageal ganglion (sb.g.), which is very closely connected to the left and right pleural ganglia. The small buccal ganglia (b.g.), which are united by a commissure, lie beneath the oesophagus in front of the cerebral ganglia to which they are attached by slender connectives.

The visceral ganglia lie one on each side of the oesophagus at the base of the mantle cavity. The right is elongate and the left is much shorter. A very similar arrangement has been described in *Cymbium melo*.

The nerves originating from the cerebral ganglia include most of the nervous supply to the proboscis. There are 3 main proboscidial nerves. A dense cluster of nerves (ci) originates at the anterior edge of each ganglion and runs dorsal to all the other anterior nerves alongside the oesophagus to the odontophore and pharynx. A single nerve (cii) emerges just outside the 1st group and supplies the ventral part of the odontophore and posterior wall of the pharynx. A 3rd nerve (ciii) originates in the antero-lateral part of the ganglion and supplies the retractor muscles of the proboscis. Also, these are innervated by a few small nerves arising laterally from the cerebral ganglia. The other cerebral nerves also supply the anterior parts of the animal. These include the anterior integumentary nerves which arise in front (civ) and run to the anterior body wall on each side. A pair of tentacular nerves (cv) supply the tentacles and head lobes, and along-side them, are very slender optic nerves (cvi) which run straight to the eyes.

The pleural ganglia give rise to a number of integumentary nerves (pl.) and, in addition, the large siphonal (siph.n.) and columellar (col.n.) nerves arise from the left pleural ganglion. The buccal ganglia have 3-4 pairs of anterior nerves (b.n.) which innervate the odontophoral muscles. Posteriorly (b.n.p.), a single nerve from the left buccal ganglion runs to the gland of Leiblein and one from the right supplies the mid-oesophagus and the sphincter of the gland of Leiblein. The 4 main nerves originate from the right end of the supra-oesophageal ganglion. The innermost nerve (vis.n.) forms half of the visceral loop and the other 3 make up the osphradial nerves (os.n.). The sub-oesophageal ganglion is practically subdivided by the widely separated bases of the 2 large nerves arising from it. These nerves are the lower (right) half of the visceral loop (vis.n.) and the right pallial nerve (pal.n.) which, accompanied by a smaller nerve supplies the posterior part of the mantle.

The pedal ganglia give off many lateral, posterior and anterior nerves, but only the main anterior (a.p.n.) and posterior (p.p.n.) branches are shown in the figure. The right pedal ganglion gives rise to a large penial nerve in the male.

A few slender nerves arise from the left visceral ganglion and these innervate the body wall. The nerves emerging from the larger right ganglion supply the organs of the visceral mass.

A pair of otocysts lie alongside the posterior portion of the pedal ganglia. Each is a vesicle about 30 μ in diameter and lies in a thick capsule of connective tissue. The sensory cuboidal epithelium has a fringe of sensory hairs and the lumen contains a single, large otolith.

DISCUSSION

Alcithoe is well suited to a burrowing mode of life, although it is not as efficient as some burrowing prosobranchs, e.g., some Naticidae and Olividae. The long anterior siphon, streamlined shell and body, and the loss of the operculum together with the posterior exhalant aperture, have required little departure from the normal rachiglossan pattern. The head flap is a peculiar volute modification to burrowing, other volutes showing an essentially similar arrangement of the head-foot, though minor variations do occur. In the most primitive living volute, *Neptuneopsis gilchristi*, the tentacles are large and there is a deep notch in the middle of the head-lobe suggesting that the

cohesion of the tentacle bases seen in most other volutes has not yet taken place. A large operculum is also present and there are no siphonal appendages (Woodward, 1900; Pace, 1902). A cleft in the middle head-lobe is also seen in another primitive volute, *Voluticorbis*, and this has no siphonal appendages, although as in most other volutes an operculum is not present. *Voluta musica* and *Lyria deliciosa* have an operculum and there is only a slight indication of a bifurcation of the head-lobe (Pace, 1902). The siphonal appendages are both large, but the right one is larger. Certain species of *Aurinia* also have a bilobed head and only the left siphonal appendage (Clench & Turner, 1964). The external features of the majority of the Volutidae, however, are similar to those of *Alcithoe*. The extension of the mantle over the outer parts of the shell is not a common feature of the Volutidae, though it is seen in *Zidona dufresnii* (Donovan) (D'Orbigny, 1847).

The migration of the primitive anteriorly facing pallial opening to its position in the Volutidae on the right side is probably correlated with the burrowing habit. This arrangement allows not only for a more efficient means of closing off the pallial cavity, but also for the ready disposal of waste products behind the widest part of the body. Thus, waste is carried away as the animal moves through the substratum rather than being forced back into the exhalant opening.

The carnivorous mode of life has imposed on the gut of *Alcithoe* several important modifications. The obvious modifications of the primitive prosobranch gut include the formation of a proboscis, simplification of the radula and stomach, the separation of the oesophageal gland from the alimentary canal to form a gland of Leiblein, and a shortening of the intestine.

The gut of *Alcithoe* has become more specialized than that of well known neogastropods such as *Buccinum* (Dakin, 1912; Graham, 1939) and *Nucella* (Graham, 1939; Fretter & Graham, 1962) in several features. These include the greater development of muscle around the oesophagus, resulting in more peristaltic transportation of food and hence more efficiency, and the development of a crop in which the food is initially broken down by the enzymes of the gland of Leiblein. This latter modification has allowed the evolution of a very efficient sorting mechanism in the stomach not seen in any other mesogastropods studied to date.

The gland of Leiblein in other members of the Volutidae is generally of similar structure to that of *Alcithoe*, at least in external features. The shape of the gland of Leiblein of 4 species belonging to 4 subfamilies is shown by Clench & Turner (1964). Their appearance is basically similar in all cases, although *Voluta musica* has a bulb-like terminal portion. *Harpovoluta* has a large, almost globose gland of Leiblein (Eales, 1912), while that of *Voluticorbis* is brown and thin-walled like that of *Buccinum*. *Voluticorbis* is clearly one of the most primitive of the described volutes, possessing such features as a triserial radula, a short, thin-walled gland of Leiblein, absence of siphonal appendages and a divided middle head lobe (see Woodward, 1900). A dilated, convoluted portion of the middle oesophagus is found behind the nerve ring before the opening of the gland of Leiblein. This region is probably partially homologous with the anterior region of the gland of Leiblein in the rest of the volutes, for by the fusing of the peaks of the dorsal folds, the long tubular part of the gland of Leiblein has almost certainly been formed. A similar long portion of the middle oesophagus with its highly glandular dorsal folds occurs in the Muricidae (Graham, 1941) where the cytology is similar. In addition, homology of the posterior part of the gland of Leiblein of *Alcithoe* with the entire gland of the Buccinidae and Muricidae is suggested by the cytology and the presence of the ventral folds in this area alone.

The gland of Leiblein is probably the main source of enzymes used in the breakdown of the food in the crop. Marche et al. (1961) observed pharmaco-dynamic effects after the injection of a gland of Leiblein extract from *Cymba pepo pepo* (=*Cymbium patulum* Broderip) into a dog.

The loss of the primitive excretory function of the digestive gland may be correlated in part with the presence of an excretory anal gland. Evidence for this supposition is that dark refringent granules like those in the anal gland epithelium are found in amoebocytes around the digestive and the anal glands in *Alcithoe*, and in certain other neogastropods (Smith, 1967).

There are some features of the reproductive system that are of special interest. The minute eggs with the large amount of albumen and virtually no yolk is an unusual situation which should be followed with further investigation.

The tubules forming the accessory seminal receptacle probably represent a supplementary mechanism for discharging waste albumen and sperm into the ingesting gland and, in addition, may store sperm. Similar sperm storing pouches that are possibly homologous are found on the dorsal wall between the capsule gland and albumen gland of *Olivella verreauxi* (Duclos) and *Oliva sayana* Ravenel (Marcus & Marcus, 1959). These have been described as seminal receptacles, while the ingesting gland (bursa copulatrix of Marcus & Marcus), although in the median position between the 2 glands, has a separate duct leading to the anterior end of the oviduct. Marcus & Marcus consider that the 'bursa copulatrix' of these species is analogous with the anterior bursa of Fretter's stenoglossans, while a small pouch on the anterior end of the pallial oviduct is held to be the homologue. They also suggest that the seminal receptacle (the median sperm pouches) is homologous with the ingesting gland. Marcus & Marcus do not however suggest any homology for their bursa copulatrix. From the situation in *Alcithoe* the bursa copulatrix of *Oliva* and *Olivella* would seem to be homologous with the ingesting gland and the sperm pouches with the accessory seminal receptacles of *Alcithoe*. The separate bursal ducts of *Oliva* and *Olivella* are probably derived from the closing off of the ventral channel, to achieve complete separation of sperm and egg conduction. The more primitive situation exists in *Alcithoe* and the other neogastropods described, in which these conducting channels are incompletely separated. The duct of the ingesting gland is usually of a very different structure from the rest of the gland. According to Fretter (1941) this is due to the modification of the distal epithelium, the original epithelium being retained in the duct. Another possibility is that the ingesting gland has been derived from a median bursa copulatrix, such as exists in some rissoids, as was suggested by Johansson (1957). The duct and other sperm-storing structures could, alternatively, be derived from a median seminal receptacle that has fused with the bursa copulatrix. Developmental and further comparative anatomical information will no doubt lend support to one or other of these possibilities.

The male genital ducts of no other volutes have been examined in detail. Woodward (1900) has noted, however, that the entire pallial duct of *Adelomelon ancilla* is a long groove. Clench & Turner (1964) show that the seminal vesicle of *Odontocymbiola americana* is a narrow, convoluted tube and therefore unlike that of *Alcithoe*. The prostate of the former species is an enclosed, narrow tube embedded in the body wall. Its penis also differs from that of *Alcithoe* in being massive, with a coiled penial duct opening at the end of a papilla.

The structure of the kidney of *Nucella lapillus* (Fretter & Graham, 1962; fig. 153) and *Buccinum* (Dakin, 1912) differs in not having the ventral and dorsal glandular areas

separated. In these species they are dove-tailed and known as the primary and secondary lamellae respectively. In the volutes and *Oliva* these 2 areas have become separated, thus representing a higher degree of development (Perrier, 1889).

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TENELLIA ADSPERSA, A NUDIBRANCH NEW TO THE AZOV SEA, WITH NOTES ON ITS TAXONOMY AND ECOLOGY

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ABSTRACT

An opisthobranchiate mollusk from the Azov Sea, previously called *Stiliger bellulus* (D'Orbigny) [Sacoglossa] in Turpaeva (1963), is in fact the nudibranch *Tenellia adspersa* (Nordmann, 1845). A taxonomic review of this species has revealed the priority of Nordmann's name, and that *Embletonia pallida* Alder & Hancock 1854 is a junior synonym. The wide geographic range of *T. adspersa* and its rapid occupation of new biotopes is due to the extreme euryhalinity of this species, its eurythermity, the diversity of its hydroid diet, the nearly complete suppression of the pelagic stage in development, and the possibility of passive transport of egg-masses and adults by ships.

INTRODUCTION

Until now no records of Nudibranchia were known from the Azov Sea. Three species of the genus *Retusa* (Cephalaspidea) and *Limapontia* sp. (Sacoglossa) were the only opisthobranchs mentioned in the detailed catalogue of the fauna of free-living invertebrates of Azov Sea by Mordukhai-Boltovskoi (1960). Turpaeva (1963) dealt with a small opisthobranchiate mollusk from the fouling of the water-intakes and technical water-piping on the shore of the Azov Sea. This mollusk, identified by V. D. Chukhchin as the sacoglossan *Stiliger bellulus* (D'Orbigny), was described by Turpaeva as feeding upon hydroids. Since all Sacoglossa are known to be exclusively herbivorous, I suspected that the identification was incorrect. My examination in September 1968 of Dr. Turpaeva's material of 1963, and the inspection of additional material collected in 1966 and 1968 and kindly placed at my disposal by her, revealed that the specimens called "*Stiliger bellulus*" were in fact the nudibranch *Tenellia adspersa* (Nordmann, 1845)[1].

SYSTEMATICS

Tenellia adspersa (under the name of *Tergipes adspersus*) was originally described from Odessa on the Black Sea by Nordmann in 1845. Four years later (1849) Schultze (under the name of *Tergipes lacinulatus*) described the development of the same species from the Baltic Sea. Subsequently Alder & Hancock (1854) obtained this species from the British coast (the shore of Birkenhead) and described it as a new species, *Embletonia pallida*, a name which later was used by most authors (see synonymy below).

Nordmann's work mainly concerns another species, *Tergipes edwardsii* Nordmann, 1845 (now *Tergipes tergipes* Forskål, 1775) (Starobogatov, pers. comm.), and probably this was the reason that Nordmann's description of *T. adspersa* was unnoticed by almost

[1]In the recent experimental work of Turpaeva (1969) this mollusk already appears under the true name.

all later Russian and foreign authors[2]. Yet the description and excellent figures given by Nordmann (1845) leave no doubt that *Embletonia pallida* Alder & Hancock and *Tergipes adspersus* Nordmann are one and the same species.

For a long time this species was considered to belong to the genus *Embletonia* Alder & Hancock, 1851 (Eliot, 1910; Odhner, 1907, 1939; Hoffmann, 1926; Winckworth, 1932; etc.). The genus *Embletonia* was based on the type species *Embletonia pulchra* (Alder & Hancock, 1844). Pruvot-Fol (1954) revealed the heterogeneous structure of the older concept of the genus—*Embletonia*, which included both *E. pulchra* (with 1 ceras without a cnidosac in a row on each side of the back) and *E. pallida* (with more than one papilla with true cnidosacs in a row on each side). Pruvot-Fol placed *E. pulchra* and *E. pallida* in 2 independent genera, retaining for the latter species the genus *Tenellia* Costa 1865, created by Costa for his new species, *Tenellia mediterranea* (=*T. adspersa* Nordmann)[3]. However Pruvot-Fol, probably by mistake, indicated *Tergipes adspersus* Nordmann[4] as a synonym of *E. pulchra*, not of *E. pallida*, in spite of Nordmann's figures which clearly show 2 cerata in a row on each side for this species.

Current anatomical studies have revealed that *Tenellia* is not only a distinct genus, but that *Tenellia* and *Embletonia* are members of 2 different families. *Tenellia* is closely related to the genera *Catriona* and *Cuthona* of the Cuthonidae, which also includes the aberrant *Subcuthona* (Baba & Hamatani, 1963). *Embletonia* is a member of the family Tergipedidae (Baba, 1959).

Synonymy of *Tenellia adspersa*

Nordmann, 1845, p 498, pl. 1, figs. 4–5 (*Tergipes adspersa*); Schultze, 1849; p 268, text-figs. 1–11 (*Tergipes lacinulatus*); Alder & Hancock, 1854, p 105 (*Embletonia pallida*); Alder & Hancock, 1855, Pt. 7, p 52, Appendix, p xii, Suppl. pl. 47, fig. 29 (*Embletonia pallida*); Meyer & Möbius, 1865, p 17, pl. 1 (*Embletonia pallida*); Costa, 1866, p 76, pl. 3, fig. 7 (*Tenellia mediterranea*); Kent, 1869, p 109, pl. 8 (*Embletonia grayi*); Gray, 1869, p 247 (*Embletonia grayi*); Mörch, 1871, p 184 (*Embletonia? pallida*); G. Sars. 1878, pl. 16, fig. 11 (*Embletonia pallida*); Herdman, 1886, p 276 (*Embletonia pallida*); Odhner, 1907, p 30, 81 (*Embletonia pallida*); Eliot, 1910, p 171, pl. 6, figs. 1, 2 (*Embletonia pallida*); Lφyning, 1922, p 65, text-figs. 44-50, pl. 3, fig. 13 (*Embletonia pallida*); Iredale & O'Donoghue, 1923, p 207 (*Embletonia pallida* and *Embletonia grayi*); Naville, 1925, p 812 (*Embletonia pallida*); Hoffmann, 1926, p 18 (*Embletonia pallida*); Winckworth, 1932, p 237 (*Embletonia pallida*); Engel, 1936, p 107 (*Embletonia pallida*); Rasmussen, 1944, p 207, figs. 15–20 (*Embletonia pallida*); Jaeckel, 1952, p 28 (*Eubranchus pallidus*); Vannucci & Hosoe, 1953, p 103, pls. 1–6 (*Embletonia mediterranea*); Pruvot-Fol, 1954, p 413, fig. 160 (*Tenellia ventilabrum*); Marcus & Marcus, 1955, p 238, pl. 38, figs. 23–31 (*Embletonia pallida*); Marcus & Marcus, 1960, p 180, fig. 80 (*Tenellia pallida*); Jaeckel, 1961, p 140, fig. 2 (*Embletonia pallida*); Swennen, 1961, p 217 (*Embletonia pallida*); Gomoiu, 1961, p 1251, text-fig. 4B (*Tergipes*); Coomans & De Coninck, 1962, p 1 (*Embletonia pallida*); Baba & Hamatani, 1963, p 337, text-fig. 1 (*Tenellia pallida*); Chukhchin, *in* Turpaeva, 1963, p 197 (*Stiliger bellulus*); Chukhchin *in* Simkina, 1963, p 218 (*Stiliger bellulus*); Chukhchin *in* Starostin &

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[2]Curiously enough Schultze (1849) payed no attention to Nordmann's description and figures of *T. adspersa*, although he often cited this author in connection with *Tergipes edwardsii*. The fact that *T. adspersa* and Schultze's "*T. lacinulatus*" are identical is obvious.

[3]Nordmann's figures of *T. adspersa* and Costa's of *T. mediterranea* are almost identical (Costa, 1866, pl. 3, fig. 7 and Nordmann, 1845, pl. 1, fig. 4). Figs. 1 and 2 in the present paper show photographs of the original figures of Nordmann.

[4]The generic name given by Nordmann (1845), Schultze (1849) and more recently by Chukhchin (1960) and Gomoiu (1961) is clearly erroneous; the symmetrical disposition of the rows of cerata with more than one papilla in each row and the absence of oral tentacles, clearly seen on the figures in the works of Nordmann, Schultze and Gomoiu, are not characters of Cuvier's (1805) *Tergipes*.

Turpaeva, 1963, p 149 (*Stiliger bellulus*); Steinberg, 1963a, p 65 (*Tenellia pallida*); Steinberg, 1963b, p 72 (*Tenellia pallida*) Chukhchin *in* Simkina, 1967, p 102 (*Stiliger bellulus*); Ławiński, 1968, p 410, figs. 1–6 (*Embletonia pallida*); Turpaeva, 1969, p 415 (*Tenellia adspersa*).

Short description of *Tenellia adspersa* from the Azov Sea[5]

The branchial papillae are arranged in 2–6 rows on each side, about 2–3 cerata (most often one large and one small) in the largest rows. The general body colour of preserved specimens is translucent grayish-white, sprinkled with minute black spots. The branchial papillae are opaque with white cnidosacs at the tips. The foot has rounded anterior corners and tapers to a blunt tail. The large head widens anteriorly and bears lateral lobe-like processes, which are often quite inconspicuous, but are sometimes more pronounced, attaining 1/3 the length of the rhinophores. The rhinophores are simple, smooth, long and thin. The acleioproctic anus is situated on the right side. The genital aperture is located just under the 1st row of papillae on the right side.

The jaw plates are narrow, almost triangular; the masticatory edges are without denticles. The radula formula is 30–43×0.1.0. Each tooth is translucent, broadly horseshoe-shaped, and has a strong, somewhat prominent median cusp with close-set denticles on each side (Figs. 3, 4). The shape of the teeth, their sizes and the number of denticles per tooth is variable within each radula. The teeth increase greatly in size from the oldest to the most recent parts of the radula; the smallest worn teeth are narrow and have 4 denticles on each side of the median cusp, whereas the largest (and youngest) plates are broad, nearly pectinate, and have 9–11 denticles on each side.

The ovotestis consists of a few acini, clearly seen through the transparent integument. The 2 main characters of the distal genital organs are: (1) the tip of the penis bears a cuticular stylet (Fig. 5), and (2) there is a large oval glans opening at the base of the penis.

The egg masses of *Tenellia adspersa* from the Azov Sea are attached to hydroids in the form of minute oval gelatinous transparent sacks. The number of eggs in 1 egg mass varies from 2–3 to 40 (Turpaeva, 1963)[6]. Development is direct; the veligers remain in the egg capsules, transforming into crawling larvae which discard their shells before leaving the egg mass. The period from spawning to hatching lasts 4–5 days (Turpaeva, 1963).

DISTRIBUTION

Tenellia adspersa is mainly a brackish-water animal, although it also occurs both in waters of normal oceanic salinity and in quite fresh water. It is a boreal species with a wide distribution. It has been recorded from Lofoten Islands and southwards along the Norwegian coast (Sars, 1878; Odhner, 1907; Lφyning, 1922), in Denmark (Mörch, 1871; Rasmussen, 1944), in the Baltic Sea up to the Gulf of Finland (Jaeckel, 1952; 1961; Ławiński, 1968; Hoffmann, 1926; Meyer & Möbius, 1865), along the coasts of the North Sea and in brackish inshore waters of the Netherlands and Belgium (Engel, 1936; Swennen, 1961; Coomans & DeConinck, 1962), in British waters and in western

[5]Only specimens preserved in alcohol were examined. According to Turpaeva (1963) the living slugs were up to 5.5 mm in length.

[6]These data are not only from the specimens maintained in water (S=8‰) normal for the region of investigation (Azov Sea near the city of Zhdanov), but also those from specimens kept in diluted and concentrated sea water.

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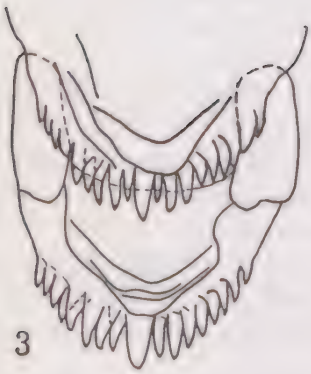

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FIGS. 1 and 2. Photographic copy of Nordmann's (1845) original figures (pl. 1, figs. 4, 5).

FIGS. 3, 4. Radular plates of *Tenellia adspersa* from the Azov Sea. FIG. 5. Penial stylet of *T. adspersa* from the Azov Sea.

Scotland (Alder & Hancock, 1855; Kent, 1869; Herdman, 1886; Swennen, 1961), along the Atlantic coast of France (Naville, 1925), and in the Mediterranean near Banyuls-sur-Mer (Marcus & Marcus, 1955), Marseilles and Naples (Pruvot-Fol, 1954; Costa, 1866). This species has been recorded in the Black Sea from the northeast Rumanian coast off Constanza (Gomoiu, 1961) and from the USSR coasts near Sebastopol and Odessa (Nordmann, 1845; Chukhchin, 1960). In the Sea of Azov this species was found near the city of Zhdanov and in the Kerch Strait (Turpaeva, 1963; Starostin & Turpaeva, 1963). *T. adspersa* has been recorded from Japan (Mukaishima, Baba & Hamatani, 1963), along the Pacific coast of North America (from San Francisco Bay to Monterey Bay, Steinberg, 1963a, b) and from the brackish waters of Brazil (Vanucci & Hosoe, 1953; Marcus & Marcus, 1960).

ECOLOGY

Tenellia adspersa is an intertidal species which is restricted exclusively to the shallow water zone, crawling among seaweeds and stones overgrown with hydroids, and in the hydroid fouling of marine water piping, harbour constructions and submerged timber-balks of docks. *T. adspersa* appears in considerable numbers in June in the water supply system and on experimental panels exposed in the Sea of Azov in the region of the city of Zhdanov (Starostin & Turpaeva, 1963; Simkina, 1963). In 1961 the egg masses of this mollusk were still seen in the hydroid fouling on experimental panels up to November. Simkina (1963) counted more than 7000 full-grown specimens (length=4–5 mm) of *T. adspersa* from a *Perigonimus megas* colony weighing 100 g.

According to Turpaeva's (1963) experiments, Azov Sea specimens endured with little noticeable effect a salinity range of 3 to 40‰. Specimens of the 2nd generation that were reared to adults in 35‰ salinity not only survived at 50‰ for 10 days, but even produced egg masses.

Tenellia apparently can live under a wide range of temperatures since it occurs in the Mediterranean near Naples and Banyuls-sur-Mer and at the same time " Beide Arten (*Tergipes edwardsii* and *T. adspersus*) kommen während des ganzen Jahres und so lange das Meer nicht gefroren ist, unfern des Ufers von Odessa vor " (Nordmann, 1845, p 500).

The feeding intensity of *Tenellia adspersa* is rather high, its extreme voracity being noticed long ago by Nordmann (1845) and Kent (1869). The experiments of Turpaeva (1963) showed that one specimen (length 5 mm) of *T. adspersa* can destroy up to 100 adult hydrants of *Perigonimus megas* in 24 hrs. The known food organisms[7] used by *T. adspersa* are *Laomedea longissima* (Pallas) (Swennen, 1961); *Laomedea loveni* Allman (Rasmussen, 1944; Jaeckel, 1952; Swennen, 1961); *Campanularia geniculata* (Linnaeus) (Schultze, 1849); *Cordylophora caspia* (Pallas) Jaeckel, 1952; Swennen, 1961; Coomans & De Coninck, 1962; Ławiński, 1968); *Cordylophora lacustris* Allman (Kent, 1869; Naville, 1925); *Perigonimus megas* Kinne (Simkina, 1963; Starostin, 1963; Starostin & Turpaeva, 1963; Turpaeva, 1969); and *Protohydra leuckarti* Greff (Marcus & Marcus, 1955). It is evident from this list that *T. adspersa* feeds mainly on hydroids of the Order Leptolida (on both suborders Thecophora and Athecata), but also on free-living species of the Order Hydrida (*Protohydra leuckarti*). The latter is the food organism of *T. adspersa* inhabiting the weedless sand bottom at Banyuls (Marcus & Marcus, 1955).

DISCUSSION

The wide geographic range of *Tenellia adspersa* very probably depends to a great extent on the passive transportation of adults and egg masses by ships. The high intensity of spawning (Turpaeva, 1963), the shortening or complete absence of a free-swimming veliger stage (especially in waters of lower salinity) and the diversity of hydroid diet increase the possibility of survival and the rapid occupation of new biotopes by this species. *T. adspersa* often has been recorded from boat harbours (in the hydroid fouling of beams and piles of boat landings) (Swennen, 1961; Coomans & De Coninck, 1962; Steinberg, 1963a). Considering that *T. adspersa* is common in the Black Sea and that constant navigation exists between the cities of Kerch and Zhdanov, the penetration of *T. adspersa* into the Sea of Azov from the Black Sea by means of ships is not only possible,

[7]Hydroid names follow Naumow (1960).

but very probable. The low salinity of the Azov Sea is not an obstacle for this nudibranch enduring equally well at 12‰ in the harbour of Copenhagen (Rasmussen, 1944), 5‰ in Martwa Wisla River (Ławński, 1958) and even the nearly fresh waters around Amsterdam, the Zuidersee (Engel, 1936) and the Thames at Victoria Docks (Kent, 1869). Moreover, specimens in the Azov Sea which inhabit the fouling in lattices of pipe lines show that this species can stand rather rapid current (0.8–2.4 m/sec.) (Starostin & Permittin, 1963).

ACKNOWLEDGEMENTS

I wish to express my sincere thanks to Professor Z. A. Filatova for encouragement, criticism and constant interest in my work. I am indebted to Dr. E. P. Turpaeva for the specimens of *Tenellia adspersa* on which this article is based.

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Malacological Review, 1970, 3: 175–183

BRIEF COMMUNICATIONS

* * * * * * *

COMPARATIVE GROWTH AND MORPHOLOGY OF SOME VENERID LARVAE (BIVALVIA, VENERIDAE)[1]

The rearing of larvae of the Veneridae has been carried out in our laboratory by a method similar to that of the Bureau of Commercial Fisheries at Milford, Connecticut, U.S.A. (see Loosanoff & Davis, 1963). This method involves the induced spawning of parents by subjecting them to variations in water temperature, the use for larval culture of sterilized stagnant sea water which was changed daily, feeding of larvae with the algae *Monochrysis lutheri* and *Isochrysis galbana* and sterilization of sea water by Millipore (0.2 μ) filtration.

We used 3 species of *Venus* (*V. striatula* Da Costa, *V. fasciata* Da Costa and *V. verrucosa* Linnaeus) and 2 species of *Venerupis* (*Vr. aurea* Gmelin and *Vr. pullastra* Montagu), all of which are common to the coast of Brittany, France. *Venus verrucosa* and *Venerupis pullastra* are economically important species.

The following study deals with shell morphology during the 1st month of larval life. The water temperature was kept constant (19.5° C± 1.5° C). Measurements in micra were made with an ocular micrometer on living larvae about every 3rd day. Each sample included about 50 larvae. We did not measure all of the larvae because of their variable growth ratio, but we measured only the 10 largest shells of each sample. Therefore, delay in growth of certain individuals did not affect our measurements.

Venus striatula Da Costa (Figs. 1, 6). Parents from Morgat (Finistère); spawned on 21st June 1969. Average diameter of eggs, 54 μ. Larvae with straight hinges are seen after about 24 hrs. The umbo becomes prominent at 18 days, at which time the larvae are 210 μ in length. The umbo continues to grow but the larvae continue to look globular and the L/W ratio hardly varies.

Venus fasciata Da Costa (Figs. 2, 7). Parents from Locmariaquer (Morbihan). Spawned on 21st April 1969. Average diameter of eggs 60 μ. Larvae with straight hinges are seen after about 24 hrs. The umbo becomes prominent at 17 days, when the larva measures 196 μ in length. The length-width relationship remains almost linear.

Venus verrucosa Linnaeus (Figs. 3, 8). Parents from Brest (Finistère). Spawned on 6th June 1969. The eggs, which average 69 μ in diameter, are surrounded by a mucous envelop. Larvae with straight hinges are seen only after 36 hrs. They exhibit regular growth curves.

Venerupis aurea Gmelin (Figs. 4, 9). Parents from Brest (Finistère). Spawned on 4th June 1969. Average diameter of eggs, 63 μ. Larvae with straight hinges are seen after 24 hrs. The umbo becomes prominent when the larva measures 130 μ. At this time the angle of the growth curve decreases from 49° to 40°. This change in growth corresponds to a change in morphology of the larval shell.

Venerupis pullastra Montagu (Figs. 5, 10). Parents from Brest (Finistère). Spawned on 23rd July 1969. Average diameter of eggs, 60 μ. Larvae with straight hinges are seen after about 24 hrs. The increase in width is greater than that of the length when the larva reaches 240 μ. A corresponding change in the angle of the growth curve from 45° to 54° can be seen at that time.

As far as we know, the only morphological studies in western Europe on laboratory raised larvae of the Veneridae are those of Quayle (1952) for *Venerupis pullastra* and Ansell (1961) for *Venus striatula*. Our present report adds new data on shell shape and growth of these 2 species, as well as 3 others. We used photomicrography for our morphological studies, a method which we found to lack the precision needed for species recognition. Nevertheless, it is evident from Loosanoff, Davis & Chanley's (1966) report that it is worthwhile to study morphology of many species from different families to assess their potential for taxonomic recognition at various taxon levels. (For example, our own studies show that a characteristic of the Veneridae prodissoconchs is the asymmetrical shoulders of the shell.)

In regard to growth, growth curves show a difference between length and width at the time of metamorphosis. This variation is only slight for the 3 species of *Venus*, but it is greater for the 2 species of *Venerupis*. The study of the length/width ratio of the shell confirms these observations (Figs. 6–10).

Further studies will concern size variation of reared larvae as well as characteristics of the hinges and their teeth.

[1]Supported by research grant No. 68/56 from Centre National pour l'Exploitation des Océans (C.N.E.X.O.), Paris, France.

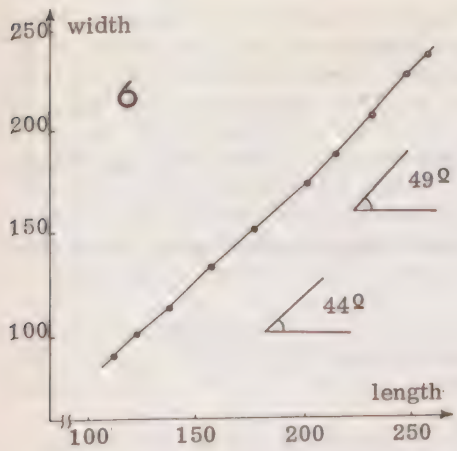
FIG. 1. Photomicrographs of larvae of *Venus striatula* during the 1st month of larval life. The first number under each illustration indicates the length of the larva in micra, the second number indicates the width.

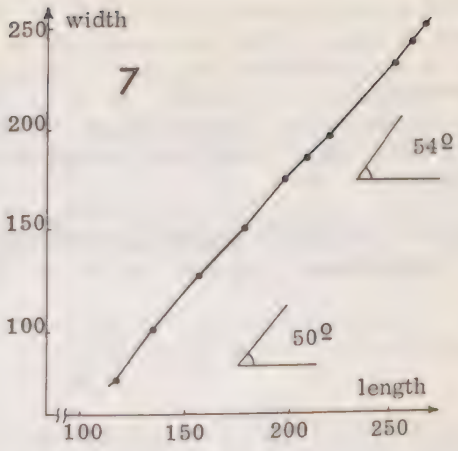
FIG. 2. Photomicrographs of larvae of *Venus fasciata* during the 1st month of larval life. The first number under each illustration indicates the length of the larva in micra, the second number indicates the width.

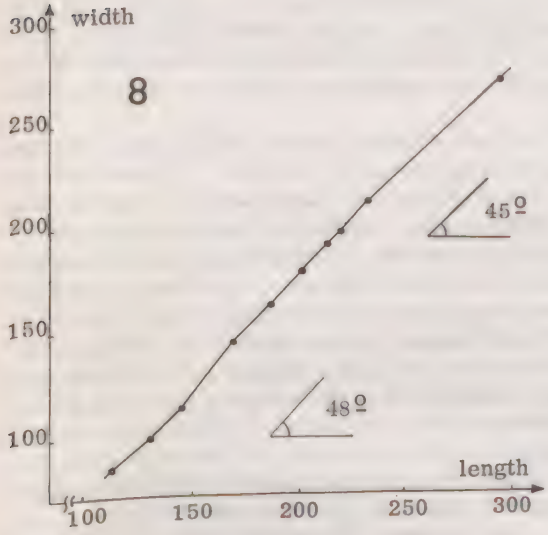
FIG. 3. Photomicrographs of larvae of *Venus verrucosa* during the 1st month of larval life. The first number under each illustration indicates the length of the larva in micra, the second number indicates the width.

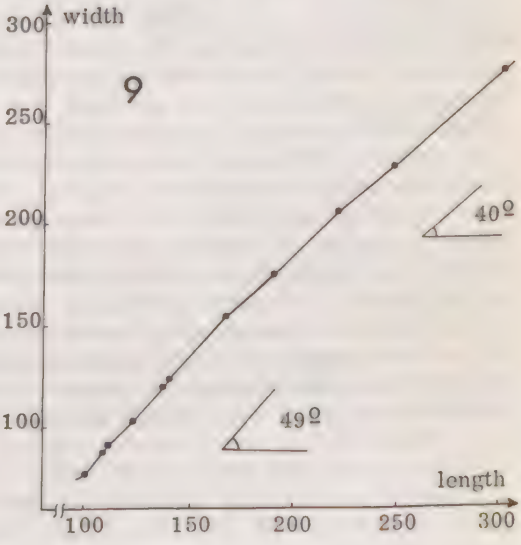
FIG. 4. Photomicrographs of larvae of *Venerupis aurea* during the 1st month of larval life. The first number under each illustration indicates the length of the larva in micra, the second number indicates the width.

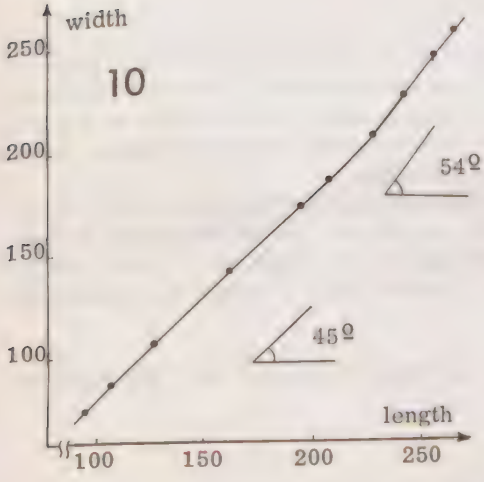
FIG. 5. Photomicrographs of larvae of *Venerupis pullastra* during the 1st month of larval life. The first number under each illustration indicates the length of the larva in micra, the second number indicates the width.











FIGS. 6–10. Length-width relations during the 1st month of larval life. FIG. 6. *Venus striatula*. FIG. 7. *V. fasciata*. FIG. 8. *V. verrucosa*. FIG. 9. *Venerupis aurea*. FIG. 10. *V. pullastra*.

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CONGRÈS DE LA SOCIÉTÉ FRANÇAISE DE MALACOLOGIE.—*COLLOQUE SUR LA SEXUALITE DES MOLLUSQUES*, Mardi 8 septembre 1970, Caen. Au cours dece Colloque des mises au point sur les problèmes fondamentaux relevant de la sexualité des Mollusques seront exposés par des rapporteurs, spécialistes de ces questions, avec l'aide d'autres spécialistes français ou étrangers, qui participeront à la discussion qui suivra chaque exposé.

Les quatre grands thèmes suivants ont été retenus: 1—*Cycles et rythmes sexuels.* Les cycles et rythmes sexuels chez les hermaphrodites et les gonochoriques, leurs rapports avec le milieu. Observation des cycles naturels et expérimentation. Rapporteur: P. Lubet (Caen). 2—*Embryologie et organogènese sexuelle.* Analyse de l'origine et de la mise en place de la gonade. Analyse de l'origine et de la morphologie des tractus génitaux. Etude expérimentale de l'organogenèse. Rapporteur: J. Tardy (Poitiers). 3—*Gamétogenèse.* Les gamétogenèses au cours des cycles sexuels: histologie et cytologie. Evolution au cours de l'ontogenèse sexuelle. Gamétogenèses comparées chez les gonochoriques et les hermaphrodites. Gamétogenèses atypiques: origine, signification, problèmes posés au cours de la différenciation cellulaire des gamètes en fonction des organismes. Rapporteur: A. Lucas (Brest). 4—*Endocrinologie de la différenciation sexuelle.* Nature endocrine des substances réglant la réalisation du sexe de la gonade et son fonctionnement chez les gonochoriques et les hermaphrodites (présentation d'un schéma général) —Nature endocrine des substances responsables de l'organogenèse et du cycle des tractus génitaux chez les gonochoriques et les hermaphrodites (présentation d'un schéma général)—Essai d'interprétation, par les mécanismes mis en évidence, des cycles et rythmes naturels. Rapporteur: W. Streiff (Caen).

Le Colloque se terminera par la projection, á 21 h., d'un film de A. Richard (Wimereux): " Biologie de la Seiche."

COLLOQUE SUR LA PALEOECOLOGIE ET L'ECOLOGIE DES MOLLUSQUES, Jeudi 10 septembre 1970, Caen. Au cours de ce Colloque les sujets retenus seront traités de façon à établir des liens entre la paléoécologie et l'écologie. C'est en effet l'un des avantages de notre Société de pouvoir aborder de tels sujets de synthèse, puisqu'elle regroupe des paléontologistes et des biologistes. Après l'exposé d'un rapporteur, une large discussion est prévue entre spécialistes.

Les quatre grands thèmes suivants ont été retenus: 1—Paléoécologie et écologie des mollusques des sédiments meubles marins. Rapporteurs: C. Babin et M. Glémarec (Brest). 2—Paléoécologie et écologie des mollusques dans les complexes récifaux coralliens. Rapporteurs: J. C. Fischer et B. Salvat (Paris). 3—Mollusques continentaux du Quaternaire. Rapporteurs: Truc et Villain (Lyon). 4—Ecologie des Ammonoïdes.

Le Colloque se terminera par une conférence, à 21 h., de Mme G. Termier sur " l'évolution de l'écologie des Mollusques pendant les temps géologiques."

SOCIÉTÉ FRANÇAISE DE MALACOLOGIE, *55 rue Buffon, 75-Paris 5e, France.*

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UNITAS MALACOLOGICA EUROPAEA IV EUROPEAN MALACOLOGICAL CONGRESS—The Fourth European Malacological Congress will be held in Geneva, Switzerland, from September 7 to 11, 1971. It will follow a 1 day meeting of museum curators in charge of molluscs, devoted to the discussion of curatorial problems and collaboration. The meetings will take place in the new Museum of Natural History and in the University buildings. All malacologists are cordially invited.

The Congress fee is S. Fr. 30 (ca. US$ 7.00) for members and corresponding members of U.M.E., S.Fr. 40 (ca. US$ 9.00) for non-members, and S.Fr. 15 (ca. US$ 3.50) for students and accompanying persons.

Accommodation will be arranged by the Tourist Office in hotels and the Student Hostel. If you are interested and have not received the circulars, please contact the president, Dr. E. Binder, for more detailed information. Address: Dr. E. Binder, IV European Malacological Congress, Museum of Natural History, CH-1211 Geneva 6, Switzerland.

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SYMPOSIUM ON INDIAN MOLLUSKS AND MALACOLOGY—A symposium on Indian mollusks and Indian malacology will be held at Porto Novo, Tamil Nadu (Madras) State, India on October 4th, 5th and 6th, 1971. The headquarters of the Symposium will be at the Centre for Advanced Study in Marine Biology, Marine Biological Station of Annamalai University, Porto Novo (P.O.). Although research papers will be invited, special emphasis will be placed on reviews of past malacological research, the status of current information, the direction of present work, and desired goals for future research. All aspects of the biology (including paleontology) of mollusks will be considered.

The Symposium will be sponsored jointly by the Centre for Advanced Study in Marine Biology and the Society for Experimental and Descriptive Malacology. The Proceedings will be published in the international journal, *Malacological Review*.

Those interested should contact Prof. R. Natarajan, Director, Marine Biological Station, Porto Novo, Tamil Nadu (Madras) State, India.

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